UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

RÔLES DE L'HÉTÉROGÉNÉITÉ ET DE LA CONNECTIVITÉ DU PAYSAGE SUR LES POISSONS DU FLEUVE SAINT-LAURENT (CANADA) : VERS DE NOUVELLES UNITÉS DE GESTION ÉCOLOGIQUES

THÈSE

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« *Si les poissons sont muets, les poissonnières sont bavardes pour eux.* »

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Physicien et écrivain allemand

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Cette thèse comprend une introduction générale, trois chapitres écrits sous forme d'articles scientifiques et une conclusion générale. Le premier chapitre a fait l'objet de deux communications orales, lors de l'American Fisheries Society (Québec, août 2014) et du colloque du Centre de la Science de la Biodiversité du Québec (Montréal, octobre 2015). Il a aussi fait l'objet d'une affiche présentée au regroupement stratégique Ressources Aquatiques Québec (Rimouski, novembre 2013). Le premier chapitre a été accepté en octobre 2017 dans la revue *Hydrobiologia* :

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RÉSUMÉ

Les activités humaines ont profondément transformé les paysages aquatiques des grands fleuves en modifiant l'hétérogénéité et la connectivité de leurs habitats. Ces transformations ont mené à la disparition et au déclin de plusieurs espèces de poissons jadis abondantes. Malgré les actions entreprises afin d'atténuer l'érosion de la diversité ichtyologique, certaines populations de poissons sont encore en situation précaire. Ce constat témoigne de la nécéssité de mieux comprendre en quoi les caractéristiques et modifications du paysage aquatique influencent l'organisation spatiale des commmunautés de poissons afin ultimement de définir des unités de gestion écologique.

La présente thèse vise à mieux comprendre le rôle des caractéristiques hydro-morphologiques et des modifications anthropiques sur l'hétérogénéité et la connectivité du paysage aquatique à différentes échelles spatiales et organisationnelles dans le fleuve Saint-Laurent (Québec, Canada). Partant d'une perspective à l'échelle de la portion fluviale portant sur la diversité des communautés de poissons, cette thèse se consacre ensuite, à une échelle spatio-temporelle plus fine, à l'accès aux habitats vitaux d'une espèce structurante pour la communauté. En effet, la connectivité entre les habitats assurant la survie des jeunes stades de vie du grand brochet (*Esox lucius*) vise à mieux comprendre le rôle des caractéristiques hydro-morphologiques et des modifications anthropiques sur le déclin de cette espèce emblématique.

Sur l'ensemble de la portion fluviale du Saint-Laurent (~350 km), un échantillonnage gouvernemental standardisé des communautés de poissons (1995-2013) a été analysé grâce à la combinaison d'analyses univariées sur les indices de diversité et d'analyses multivariées sur la structure d'abondance des espèces. Les analyses révèlent des résultats contrastés selon les indices utilisés et soulignent l'importance de considérer plusieurs facettes de la diversité. En effet, seul l'indice de diversité taxonomique révèle une augmentation graduelle de la diversité vers l'aval mettant en lumière l'importance des communautés de l'estuaire fluvial. De plus, le long de ce continuum, les analyses multivariées mettent l'accent sur l'hétérogénéité des communautés à plusieurs échelles spatiales : au sein d'unités hydro-morphologiques distinctes (par ex. corridor vs. lac fluvial vs. archipel), et entre les rives opposées de mêmes secteurs séparées par un profond chenal de navigation. Ces entités géographiques qui reflètent

une réalité écologique pourraient être utilisées par les gestionnaires de la ressource du Saint-Laurent.

De la portion étroite entre Montréal et Sorel au vaste lac Saint-Pierre (~150 km), la modélisation des habitats de nourriceries du grand brochet pour la période 1965-2013 a été couplée à un modèle de fraie existant. Les mesures de connectivité entre les frayères et les nourriceries révèlent que certaines frayères ayant un fort potentiel pour les géniteurs peuvent devenir, dans certaines conditions hydrologiques, de réelles trappes écologiques pour les œufs et les larves. Alors qu'une rapide diminution du niveau de l'eau peut assécher la majorité des frayères dans le lac Saint-Pierre, l'augmentation de la vitesse du courant (>10 $cm.s^{-1}$) dans le corridor Montréal-Sorel peut disperser les larves en dehors des bons habitats. De plus, la régularisation du fleuve Saint-Laurent et l'expansion de l'agriculture jusque dans sa plaine d'inondation ont profondément altéré les habitats et leur connectivité, de sorte que les événements hydrologiques hauts et stables, qui auraient été naturellement favorables pour le grand brochet, ont perdu leur potentiel productif. En effet, les hauts niveaux d'eau sont plus fréquemment suivis d'une rapide diminution limitant le succès de reproduction, alors que les habitats anciennement accessibles dans le haut de la plaine d'inondation sont devenus inopérants pour les poissons à cause des pratiques agricoles. Cette étude souligne aussi que la connectivité des habitats dans le lac Saint-Pierre est favorisée par des conditions hydrologiques stables lorsqu'il y a chevauchement entre les frayères et les nourriceries, ainsi que par la dispersion des larves dans de faibles courants (<10 $cm.s^{-1}$) leur permettant de rejoindre des habitats plus distants.

Les résultats de la présente thèse apportent un nouvel éclairage sur les caractéristiques et modifications du paysage aquatique qui gouvernent l'organisation spatiale des communautés de poissons du fleuve Saint-Laurent ainsi que la complétion des premiers stades de vie d'une espèce structurante pour la communauté. Ils visent à contribuer à la gestion de la ressource ichtyologique en identifiant des unités de gestion écologique à différentes échelles spatiales (par ex. les rives, les habitats interconnectés), en priorisant des sites à conserver (par ex. l'estuaire fluvial, les frayères effectives récurrentes) ou en évaluant l'efficacité d'aménagements existants (par ex. les marais aménagés). L'identification de pressions anthropiques ayant un rôle majeur sur ces processus critiques ouvre la porte à des mesures de restauration telles que la conversion de cultures agricoles et un retour vers une variation plus naturelle des niveaux d'eau. Bien qu'appliquées au fleuve Saint-Laurent et au grand brochet, les notions et les méthodes développées dans la présente thèse sont théoriquement exportables à d'autres espèces ainsi qu'à d'autres grands fleuves, à condition de calibrer et valider les modèles à leurs nouveaux contextes.

Mots clés : diversité, connectivité, grand brochet, modélisation, pressions anthropiques.

ABSTRACT

Human activities have deeply transformed the large river landscape by altering the habitats heterogeneity and connectivity. These transformations led to the decline, and the local extinction, of several fish species once abundant. Despite actions aimed at mitigating fish diversity loss, some populations are still declining. In this context, it appears essential to better understand how landscape characteristics and alterations influence spatial organization of fish communities. Such key information can ultimately allow defining sound ecological management units.

The present thesis aims at understanding the role of hydro-morphological characteristics and anthropogenic modifications on landscape heterogeneity and connectivity at different spatial scales and organizational levels in the St. Lawrence River (Quebec, Canada). The thesis starts with a large scale perspective by studying the spatial organization of fish communities within the fluvial St. Lawrence, then the focus turns on a smaller spatio-temporal scale by studying how connectivity can alter the access to vital habitats for a structuring species of the fish community. Indeed, connectivity between habitats that allows northern pike (*Esox lucius*) larvae survival is modelized to better understand the role of hydro-morphological characteristics and anthropogenic modifications on population decline of this emblematic apex predator.

Firstly, at the St. Lawrence River scale (~ 350 km), a standardized governmental fish community sampling (1995-2013) was analysed using a combination of univariate analysis on diversity indices and multivariate analysis on the structure of fish abundance. Diversity indices revealed contrasting patterns that stresses the importance of considering several facets of diversity. Indeed, only the taxonomic disctincness index revealed a gradual downstream increase along the St. Lawrence River, which highlighted the high fish diversity of the fluvial estuary. In addition, along this continuum, multivariate analysis revealed how heterogeneity of fish communities is structured at different spatial scales: differences were found between distinct hydro-morphologic units (e.g. corridor vs. fluvial lake vs. archipelago), and between opposite shores of same sectors (separated by the deep navigational channel). Since the geographical units defined by the fish community architecture reflect the ecological reality along the St.Lawrence, the latter could be used by St. Lawrence managers.

Secondly, from the narrow Montréal-Sorel corridor to the vast Lake Saint-Pierre (~ 150 km), we modelled the northern pike nursery habitats for the period 1965-2013 and coupled theses to an existing spawning habitats model. The connectivity between spawning and nursery habitats revealed that some spawning areas with high potential for spawners may become, during certain hydrological conditions, mortality traps for eggs or larvae. While a rapid decrease of water discharges may dewater most of the spawning habitats in Lake Saint-Pierre, an increase of current speeds (> 10 $cm.s^{-1}$) in Montréal-Sorel corridor can flush larvae outside suitable habitats. Moreover, the St. Lawrence River regularisation and the expansion of agriculture into its floodplain have profoundly altered the habitats and their connectivity. While stable-high water discharges were theoretically favourable for northern pike recruitment, such conditions are no longer favourable as the landscape is now negatively impacted by anthropogenic alterations. Indeed, high water discharges are more frequently followed by a rapid decrease limiting spawning success, and habitats on the upper part of the floodplain have been altered by agricultural practices. In addition, our results found that habitat connectivity in Lake Saint-Pierre is favoured by stable hydrological conditions when spawning and nursery habitats overlapped, as well as by the larvae dispersal in low current speeds (< 10 $cm.s^{-1}$) allowing them to reach more distant habitats.

The present thesis shed new lights on landscape characteristics and modifications that govern spatial organization of fish communities in the St. Lawrence River and the dynamic related to early-life habitats exploitation and recruitment for an emblematic species. Our results contribute to fish management by identifying ecological management units at different spatial scales (e.g. shorelines, connected habitats), allowing priorization of sites to be preserved (e.g. fluvial estuary, recurrent effective spawning habitats) or by assessing the effectiveness of existing managements actions/tools (e. g. managed wetlands). By identifying which anthropogenic pressures led to major impacts on these critical processes, it opens the door to more efficient restoration actions such as the conversion of agricultural crops in natural habitats and the return to more natural variations of water discharges. Although the present thesis focus on the St. Lawrence River and the northern pike, the notions and methods developed herein are theorically exportable to other large rivers as well as to other species, under the condition to calibrate and validate the models used within their new context.

Keywords : diversity, connectivity, northern pike, habitat modelling, anthropogenic pressures.

INTRODUCTION GÉNÉRALE

0.1 Déclin universel des poissons d'eau douce et altération des paysages aquatiques

Au cours des dernières années, les humains ont rapidement et largement transformés les écosystèmes à l'échelle planétaire, en grande partie pour répondre aux besoins croissants en nourriture, en eau, en bois, en fibres et en carburant (MEA 2005). Ces transformations ont affecté de manière substantielle les milieux d'eau douce, qui font parties des écosystèmes les plus menacés au monde (Gleick 2003; Jenkins 2003; Collen *et al*. 2014). Alors que les poissons sont d'excellents indicateurs de l'état de santé des écosystèmes aquatiques (Harris 1995), près de 30% des espèces d'eau douce sont menacées d'extinction (Collen *et al*. 2014). Les grands fleuves, qui supportent une diversité ichtyologique élevée et qui se distinguent des autres rivières par la taille de leur bassin versant ($> 900\,000\ km^2$) et leur débit annuel ($> 7\,500\ m^3.s^{-1}$) (Bethemont 2003), ont vu plusieurs de leurs espèces décliner ou disparaître (par ex. Mississippi, Volga, Danube, Gange; Usova 2004; Holcík 2009; Sparks 2010; Das *et al*. 2013). Parmi les 97 espèces de poissons inventoriées dans la portion fluviale du Saint-Laurent, l'abondance de plusieurs d'entre elles d'importances écologique et économique telles que l'anguille d'Amérique, la perchaude et le grand brochet s'affaiblit (Smith *et al*. 2007; Verreault *et al*. 2012; de la Chenelière *et al*. 2014; Mingelbier *et al*. 2016).

La dégradation et la fragmentation des paysages aquatiques sont les principales causes du déclin et de la disparition des poissons d'eau douce (Aarts *et al*. 2004; Fischer et Lindenmayer 2007; Collen *et al*. 2014). Le paysage est défini comme un environnement hétérogène composé d'habitats ou d'écosystèmes en interaction

(Dunning *et al*. 1992; Wiens 2002). L'approche des systèmes fluviaux sous l'angle du paysage permet de considérer l'ensemble du cycle de vie du poisson, de ses besoins en habitats souvent diversifiés, et de ses réponses aux changements d'habitats principalement engendrés par les activités humaines. En effet, les usages nombreux et variés tels que la consommation en eau, le développement de la pêche, des usages urbains, industriels, énergétiques, agricoles, de voies navigables et aussi touristiques ont profondément transformé les paysages aquatiques des grands fleuves en modifiant l'hétérogénéité et la connectivité de leurs habitats (Vincent et Dodson 1999; Hudon et Carignan 2008; Mingelbier *et al*. 2008b; Foubert 2015). C'est le cas du fleuve Saint-Laurent, où la régularisation du débit a entrainé l'homogénéisation d'habitats aquatiques en amont de sa portion fluviale et a créé une rupture de connectivité en raison de la présence de barrages (La Violette *et al*. 2003). De surcroît, de nouvelles pressions, telles que l'introduction d'espèces envahissantes et les changements climatiques, s'ajoutent aux pressions existantes et complexifient le diagnostic de l'état de la ressource ichtyologique. La multitude des pressions qui agissent sur la dégradation et la fragmentation des paysages aquatiques souligne le besoin de quantifier l'ampleur de leurs effets sur l'organisation spatiale des communautés et des populations de poissons en vue de définir des unités de gestion écologiques.

La conservation et la restauration des milieux naturels visent à atténuer l'érosion de la biodiversité et le déclin des espèces (Dobson *et al*. 1997). La diversité et la structure des communautés de poissons, mesurées grâce à des indices complémentaires, sont utilisées afin d'identifier des zones prioritaires à protéger (Kanno *et al*. 2012; Maire *et al*. 2013). D'autre part, certaines espèces de poissons emblématiques font l'objet d'une attention particulière pour cibler des habitats critiques à restaurer (Barlaup *et al*. 2008; Snickars *et al*. 2010). En revanche, une mauvaise représentation de la diversité des communautés de poissons ou des processus spatiaux qui permettent la complétion du cycle de vie des espèces peut rendre inefficace la gestion de la ressource ichtyologique et aller jusqu'à la création de trappes écologiques (Williams

et al. 1996; Galat et Zweimüller 2001; Jeffres et Moyle 2012). Cette réalité force à sortir des modèles classiques de gestion, tel que la protection d'un plus grand nombre d'espèces ou d'un type d'habitat particulier, et à recourir à des approches plus intégratives et spatialement explicites afin de donner un sens écologique aux unités de gestion notamment dans des grands fleuves aux caractéristiques uniques (Vincent et Dodson 1999; Buijse *et al*. 2002; Stuart-Smith *et al*. 2013; Mingelbier *et al*. 2016).

0.2 Détection de processus écologiques à l'échelle du paysage aquatique

L'écologie du paysage a permis de faire le pont entre des disciplines bien établies telles que la géographie et l'écologie, et aussi entre la recherche et la conservation (Fausch *et al*. 2002). Ces concepts, tels que l'hétérogénéité et la connectivité, ont été traditionnellement développés dans les systèmes terrestres et ont récemment été adaptés aux systèmes fluviaux (Ward 1998; Fausch *et al*. 2002; Poole 2002; Wiens 2002). Bien que certains des concepts développés en écologie du paysage ne soient pas nouveaux en écologie aquatique, l'approche des systèmes fluviaux sous l'angle du paysage - ou « riverscape » - permet de les intégrer dans un cadre théorique plus large et spatialement plus réaliste et explicite (par ex. Falke *et al*. 2013; Massicotte *et al*. 2014).

Les caractérisitiques du paysage aquatique, tel que le degré d'hétérogénéité et de connectivité de ses habitats, s'expriment à des échelles spatiales (1 à 100 km) et temporelles (5 à 50 ans) variées et imbriquées (Fausch *et al*. 2002). Ainsi, les analyses multi-échelles visent à évaluer le rôle du paysage sur des processus écologiques qui agissent à différents niveaux d'organisation (par ex. Downes *et al*. 2000). Alors que les communautés de poissons peuvent reflèter les caractéristiques du paysage à l'échelle d'une portion de rivière (par ex. la présence de lacs fluviaux le long d'un continuum), le niveau d'organisation populationnelle permet d'évaluer le rôle du paysage à plus fine échelle spatio-temporelle (par ex. la connectivité des habitats des premiers stades de vie, Figure 0.1).

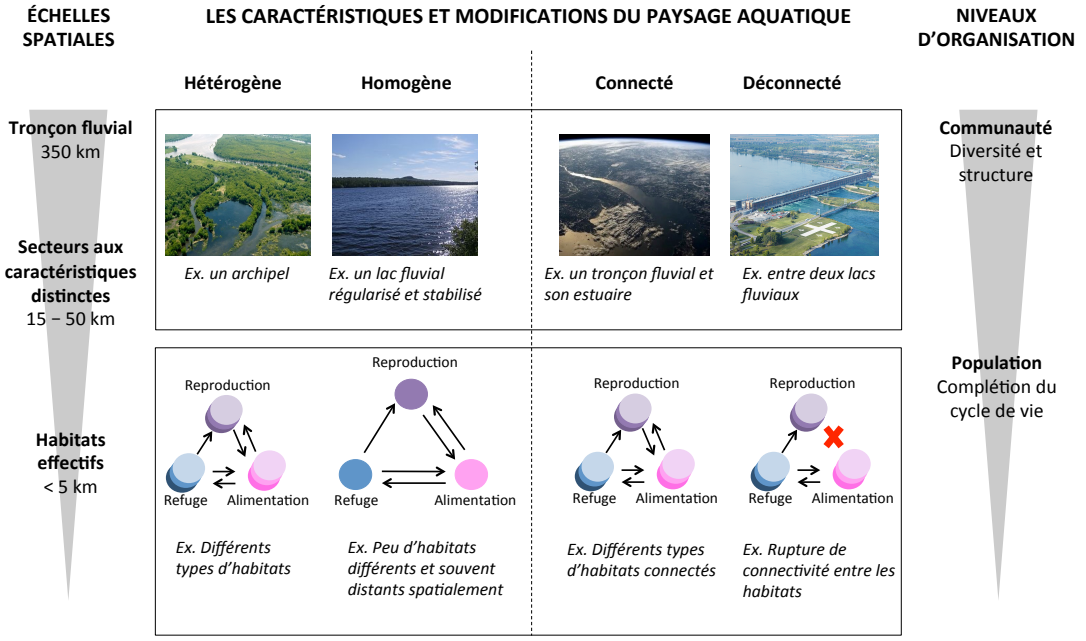

Figure 0.1 Schéma conceptuel présentant le rôle des caractéristiques hydro-morphologiques et des modifications anthropiques du paysage aquatique à différentes échelles spatiales et à deux niveaux d'organisation.

0.2.1 Niveau d'organisation : la communauté

L'écologie des communautés est décrite comme l'étude d'un niveau d'organisation biologique qui s'intéresse à « un ensemble de populations de différentes espèces vivant dans la même zone ou habitat » (Krebs 1972). Comprendre les facteurs et processus qui déterminent la structure et la diversité des communautés, variant dans l'espace et dans le temps, est un défi majeur pour les écologistes. Partant du constat que les patrons de diversité des communautés ne s'expliquent pas uniquement à l'échelle locale (c.-à-d. par les variables environnementales locales <1 km, Chase et Bengtsson 2010), le rôle des caractéristiques du paysage qui s'observe à plus large échelle (1 à 100 km) est reconnu depuis peu comme essentiel à leur compréhension. Dans les systèmes fluviaux, la diversité des communautés de poissons est influencée par la réponse des organismes, potentiellement interconnectés par la dispersion (c.-à-

d. concept de méta-communauté), à l'hétérogénéité du paysage et au degré de connectivité (Wiens 2002). Un paysage hétérogène et connecté est associé à une valeur élevée de biodiversité (par ex. Mellin *et al*. 2012; Massicotte *et al*. 2014). En effet, la mosaïque d'habitats qui composent le paysage ainsi que les connexions spatiales entre ces derniers répondent aux besoins d'un grand nombre d'espèces. À l'inverse, un paysage qui s'homogénéise et qui se fragmente est associé à une diminution de la biodiversité (par ex. Bengtsson 2010; Staddon *et al*. 2010). La réduction de la qualité des habitats et leur isolement favorisent principalement les espèces compétitrices et les espèces qui possèdent de fortes habiletés à se disperser. Les habitats sont alors composés de communautés similaires. De par leur taille et les multiples pressions qu'ils subissent, les paysages observés à l'échelle des grands fleuves sont - à divers degrés - hétérogènes, connectés, dégradés et fragmentés, ce qui complexifie le portrait de la diversité des communautés de poissons le long de leur continuum (par ex. Massicotte *et al*. 2014; Gladyshev *et al*. 2015).

La diversité des espèces peut être exprimée par divers types d'indicateurs, qui reflètent de multiples facettes de la réponse des organismes à l'hétérogénéité du paysage. Par exemple, la diversité spécifique, qui est la plus communément et traditionnellement mesurée, représente le nombre (c.-à-d. la richesse) et l'abondance relative (c.-à-d. l'équitabilité) des espèces au sein d'une communauté (Magurran et McGill 2011). La diversité taxonomique, quant à elle, exprime la distance moyenne entre les taxons qui regroupent les organismes ayant des caractères morphologiques et évolutifs en commun (espèces, genres, familles et ordres; Clarke et Warwick 1998). Plus la distance taxonomique est grande entre deux espèces (par ex. un cyprin et un salmonidé), plus la diversité taxonomique est élevée. L'intérêt d'utiliser cet indice réside dans la mise en valeur de paysages qui abritent peu d'espèces mais qui ont des caractéristiques taxonomiques très différentes. De plus en plus utilisé, le concept de diversité fonctionnelle vise à regrouper les espèces par guildes en s'appuyant sur leurs caractéristiques écologiques et d'histoire de vie (par ex. la taille, l'alimentation,

l'habitat, la mobilité; Mouchet *et al*. 2010). Comme pour la diversité spécifique, le nombre ou l'équitabilité des taxons et des guildes sont considérés dans les calculs des indices utilisés. Les différents aspects de la diversité, qui ne sont pas exhaustifs dans ce paragraphe, révèlent des informations complémentaires (par ex. Chantepie *et al*. 2011; Maire *et al*. 2013). La difficulté réside dans leur multiplicité. De plus, il faut rester prudent à l'égard d'indices sensibles à l'effort d'échantillonnage (qualité et intensité) et au nombre d'individus capturés (par ex. la richesse spécifique; Gotelli et Colwell 2001).

0.2.2 Niveau d'organisation : la population

Au sein des communautés, les populations formées par définition d'individus susceptibles de se reproduire entre eux, peuvent connaitre de fortes fluctuations d'abondance. Les changements dans l'hétérogénéité et la connectivité du paysage peuvent influencent les fluctuations d'une même population de poissons, ce qui peut se refléter au niveau de la communauté. C'est le cas des paysages aquatiques, où la dégradation et la fragmentation de leurs habitats ont été directement reliées au déclin de plusieurs espèces (par ex. esturgeon blanc; Vardy *et al*. 2013) entrainant une diminution de la diversité ichtyologique. En effet, le cycle de vie des poissons est complexe et requiert divers types d'habitats pour chaque fonction vitale (reproduction, alimentation, refuge, dispersion; Schlosser 1995). Le passage des habitats de reproduction (c.-à-d. les frayères) aux habitats de croissance des larves (c.-à-d. les nourriceries) correspond à une période critique du cycle de vie (Hjort 1914), au cours duquel le taux de mortalité est particulièrement élevé (par ex. 81-84% pour le grand brochet; Dahlberg 1979). De nombreuses théories ont été développées dans le milieu marin afin de souligner l'importance des processus spatiaux, dont la connectivité entre les frayères et les nourriceries, sur la survie des larves et le recrutement (par ex. l'hypothèse de la dérive aberrante; Houde 2008). En parallèle, ces processus sont moins bien documentés dans le domaine de l'eau douce (Falke *et al*. 2013; Ludsin *et al*. 2014; Goto *et al*. 2015).

La connectivité des habitats présente (1) une composante structurelle qui dépend de la forme, de la taille et de la position relative des éléments dans le paysage et (2) une composante fonctionnelle qui décrit la réponse des individus à ces structures en termes de mouvements, de coûts et de risques de mortalité (Baudry et Merriam 1988). Ainsi, la connectivité reflète les capacités de l'espèce (ou de la guilde) considérée qui varient à chaque stade de développement. Ayant généralement de faibles capacités natatoires, le transport passif (c.-à-d. la dispersion par le courant) contribue largement à la connexion entre les frayères et les nourriceries au stade larvaire (par ex. Dettmers *et al*. 2005; Dickey-Collas *et al*. 2009). Bien que certains éléments, naturels ou anthropiques, qui composent le paysage facilitent la connectivité entre ces deux habitats (par ex. le courant et les drains agricoles), d'autres peuvent la restreindre (par ex. les infrastructures de transport, Schiemer *et al*. 2003; Washitani 2007; Hufnagl *et al*. 2013). Sur le schéma ci-dessous (Figure 0.2), les nourriceries potentielles (#1) les plus proches de la frayère ne pourront pas être utilisées par les larves en raison d'un courant trop élevé qui restreint la connectivité entre les rives. En revanche, les larves dispersées par un faible courant pourront atteindre d'autres nourriceries potentielles localisées plus loin (#2). Ces nombreux éléments, qui délimitent l'échelle spatiale à laquelle certains processus écologiques se réalisent, complexifient le portrait de la connectivité dans de grands écosystèmes hétérogènes.

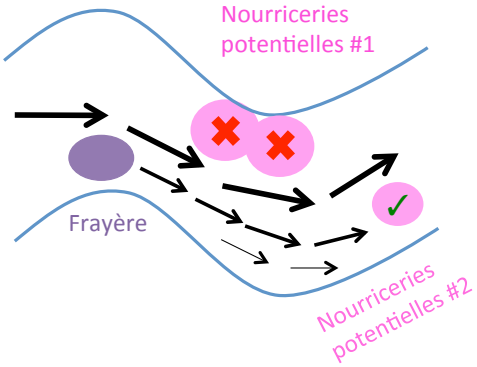

Figure 0.2 Effet du courant sur la connectivié entre une frayère, en mauve, et deux zones de nourriceries potentielles en rose.

Au-delà de la force physique permanente et directionnelle imposée par le flux d'eau, la variabilité du régime hydrologique des systèmes fluviaux (c.-à-d. l'amplitude, la durée et la périodicité du niveau de l'eau) exerce un fort impact sur la connectivité (Junk *et al*. 1989; Poole 2002; Wiens 2002; Fullerton *et al*. 2010). Les fluctuations journalières, saisonnières et interannuelles créent des écoulements dynamiques dans des paysages où la structure des éléments et leur degré de connectivité peut aussi changer rapidement. Par exemple, bien que de hauts niveaux d'eau connectent latéralement de nombreux habitats propices à la reproduction dans les plaines d'inondation, une réduction rapide de ce niveau peut soudainement assécher ou isoler ces habitats entrainant une mortalité larvaire élevée (Bayler 1991; Gorski *et al*. 2011). De plus, la modification du régime hydrologique liée à la régularisation des cours d'eau a eu des conséquences négatives sur l'ensemble de la production des poissons littoraux (Nilsson *et al*. 2005). Ces modifications ont limité l'étendue des habitats utilisés par les jeunes stades de vie, entrainant le déclin de certaines populations de poissons (par ex. Goto *et al*. 2015).

0.3 Site d'étude : le fleuve Saint-Laurent

Le fleuve Saint-Laurent est un laboratoire à ciel ouvert idéal pour mieux comprendre en quoi les changements de paysages observés dans les grands fleuves ont modifié l'organisation spatiale des communautés et des populations de poissons. Avec un bassin versant de 1 344 200 km^2, son débit moyen annuel de 12 600 $m^3.s^{-1}$ (à Québec), sa longueur de 1 197 km et son bassin de population humaine de 7,5 millions de personnes, le fleuve Saint-Laurent est considéré comme l'un des plus grands fleuves du monde (Bethemont, 2003). Il se compare à la Volga (Europe de l'Est) et au fleuve Murray (Australie) quant à sa longueur et sa superficie, ainsi qu'au Gange (Inde) et au Mississippi (États-Unis) quant à son débit (Tableau 0.1).

Tableau 0.1 Caractéristiques du fleuve Saint-Laurent et d'autres grands fleuves tempérés. À titre de comparaison, Bethemont (2003) classe le Mississippi au 3ème rang, la Volga au 15ème rang et le Saint-Laurent au 21ème rang mondial par la superficie de leur bassin et leur débit.

Caractéristiques	Mississipi	Volga	Saint-Laurent	Danube	Rhône
Pays	USA	Russie	Canada-USA [*avec les Grands lacs*]	Europe (19 pays)	Suisse-France
Superficie (km^2)	3 238 000	1 380 000	1 344 200 [*1 600 000*]	801 463	97 800
Longueur (km)	3 779	3 530	1 197 [*3 260*]	3 020	813
Débit moyen à l'embouchure ($m^3 . s^{-1}$)	18 000	8 400	12 600	6 200	1 700
Population (millions)	72	57	7,5 [*45*]	80	13 (Rhône-Mediterannée)

La physiographie du fleuve Saint-Laurent varie fortement entre l'exutoire des Grands Lacs, où il prend source, jusqu'au golfe du Saint-Laurent (Figure 0.3). Dans le cadre de la présente thèse, la portion québécoise d'eau douce localisée entre Cornwall et Québec (soit environ 400 km de long), a été étudiée. Cette portion hétérogène du Saint-Laurent comprend trois lacs fluviaux (lac Saint-Louis, lac Saint-François et lac Saint-Pierre), des sections plus étroites parsemées de nombreuses îles regroupées en archipels, et un estuaire fluvial d'eau douce (Figure 0.3). Les variations du niveau de l'eau, croissantes de l'amont vers l'aval suite aux apports progressifs des tributaires, maintiennent une plaine d'inondation le long du continuum fluvial particulièrement vaste au lac Saint-Pierre (Morin *et al*. 2005). Le fleuve draine les eaux de grands tributaires, qui coulent côte à côte et que l'on peut retracer sur de longues distances, en raison de leurs caractéristiques physicochimiques contrastées et du faible mélange latéral (Morin et Bouchard 2000). Ce n'est qu'en aval du lac Saint-Pierre, dans les rapides Richelieu entre Trois-Rivières et Québec, que le renversement du courant par les marées mélange les masses d'eau entre elles. Comparé à des fleuves dans d'autres régions tempérées, le Saint-Laurent est un fleuve diversifié qui abrite près d'une

centaine d'espèces de poissons d'eau douce. Ce nombre se compare à celui du Mississippi, alors qu'une soixantaine d'espèces ont été observées dans la Volga, le Danube, le Rhin et le Rhône et une trentaine dans la Seine (Galat et Zweimüller 2001; Belliard *et al*. 2009; Sparks 2010).

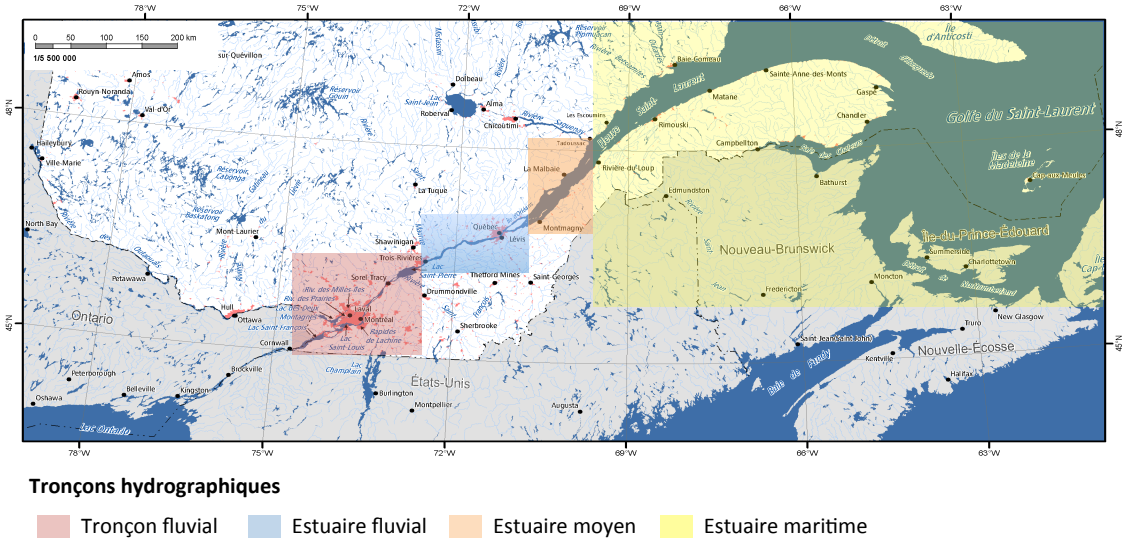

Figure 0.3 Le fleuve Saint-Laurent divisé en quatre régions hydrographiques et écologiques : le tronçon fluvial de Cornwall à Trois-Rivières, l'estuaire fluvial de Trois-Rivières à la pointe Est de l'île d'Orléans, l'estuaire moyen de la pointe Est de l'île d'Orléans à Tadoussac, et l'estuaire maritime qui comprend le golfe du Saint-Laurent.

Le fleuve Saint-Laurent est exposé à de nombreuses pressions reliées au développement du Québec moderne qui ont transformé les paysages aquatiques et mené au déclin de certaines espèces de poissons jadis abondantes. Bien que le plan de régularisation du lac Ontario, datant de 1958, ait été révisé en 2016 afin d'inclure des indicateurs environnementaux, il demeure que les effets de la régularisation de la rivière des Outaouais (depuis 1911) sont 10 fois plus importants (Morin et Bouchard 2000). En effet, avant la régularisation de l'Outaouais, le débit naturel avant 1911

(ligne bleu, Figure 0.4) engendrait une crue moyenne beaucoup plus élevé et plus longue au printemps lors de la reproduction de nombreuses espèces de poissons, en comparaison au débit régularisé actuel (ligne rouge).

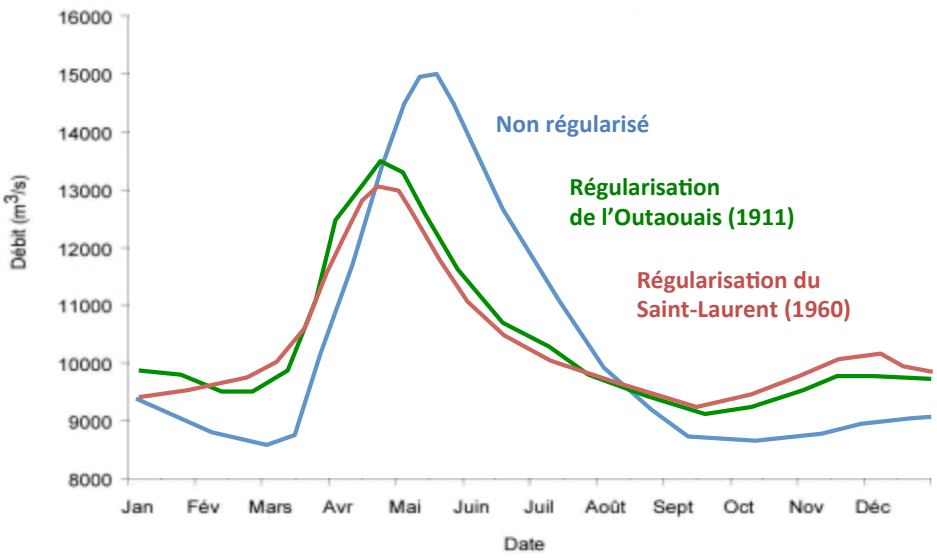

Figure 0.4 Moyenne interannuelle du débit reconstitué à Sorel pour la période 1965-2013 (Morin et Bouchard 2000).

En outre, le fleuve Saint-Laurent étant la principale voie de pénétration vers l'intérieur du continent nord-américain, l'aménagement d'un chenal de navigation (profondeur $\geq 11{,}3$ m; largeur ≈ 250 m ; vitesse du courant de 0,5-2,0 $m.s^{-1}$) a nécessité des travaux majeurs de dragage et autres ouvrages d'ingénierie dans la portion entre Montréal et Québec. Ce chenal, séparant les deux rives du fleuve fait maintenant partie du paysage du Saint-Laurent et les effets de cette barrière sur l'organisation spatiale des communautés de poissons sont encore mal connus. De plus, depuis les années 1990, la spécialisation et l'intensification des productions agricoles dans la vallée du fleuve Saint-Laurent sont responsables de la dégradation de nombreux habitats aquatiques et de la qualité de l'eau du littoral et des bassins versants (Fecteau et Poissant 2001; de la Chenelière *et al*. 2014). À cela s'ajoutent,

entre autres, les effets de rejets urbains sur la qualité de l'eau et la féminisation des poissons, les effets d'introduction d'espèces invasives sur l'homogénéisation des communautés, ou encore les effets des extrêmes climatiques sur la réduction des refuges thermiques.

0.4 Objectifs et plan de la thèse

Dans un contexte où la gestion de la ressource ichtyologique du fleuve Saint-Laurent est au cœur des priorités, la présente thèse vise à mieux comprendre le rôle des caractéristiques hydro-morphologiques et des modifications anthropiques sur l'hétérogénéité et la connectivité du paysage aquatique à différentes échelles spatiales et organisationnelles dans le fleuve Saint-Laurent (Québec, Canada). Partant d'une perspective à l'échelle de la portion fluviale portant sur la diversité des communautés de poissons (chapitre I), cette thèse se consacre ensuite, à une échelle spatio-temporelle plus fine, à l'accès aux habitats vitaux d'une espèce structurante pour la communauté (chapitre II et III). En effet, la connectivité entre les habitats assurant la survie des jeunes stades de vie du grand brochet (*Esox lucius*) vise à mieux comprendre le rôle des caractéristiques hydro-morphologiques et des modifications anthropiques sur le déclin de cette espèce emblématique. Ces changements d'échelles spatiales, temporelles, et organisationnelles (communauté et population) seront l'occasion de souligner le rôle du paysage aquatique sur des facteurs et des processus critiques qui limitent ou supportent la diversité et la productivité ichtyologique dans le fleuve Saint-Laurent. Ainsi, l'application de concepts clés à ces écosystèmes uniques, relativement à leur diversité ichtyologique et la connectivité de leurs habitats, pourra contribuer à améliorer la gestion de cette ressource.

Titre du Chapitre I : Organisation spatiale des communautés de poissons le long du fleuve Saint-Laurent : tester les gradients longitudinaux et le rôle de l'hétérogénéité du paysage aquatique.

Le chapitre I est consacré aux changements dans la structure et la diversité des communautés de poissons le long du fleuve Saint-Laurent, de Cornwall à Québec (≈ 350 km de long). Les caractéristiques du paysage, formées par contrôles géologiques, climatiques et/ou anthropiques, ont permis de définir des unités hydro-morphologiques distinctes à plusieurs échelles spatiales : les lacs fluviaux versus les corridors, les différents secteurs présentant des caractéristiques hydro-morphologiques spécifiques, et les rives opposées de chaque secteur séparées par un profond chenal de navigation. Ainsi, les rôles de l'hétérogénéité du paysage et du degré de connectivité sur les communautés de poissons ont été évalués en comparant leur diversité (spécifique et taxonomique) et leur structure d'abondance à plusieurs échelles spatiales. Bien que les écosystèmes fluviaux soient linéaires, l'hypothèse de base suggère que les changements de paysage de l'amont vers aval, tels que l'alternance de lacs, de corridors et d'un archipel, peuvent créer des dissimilarités entre les communautés de poissons du Saint-Laurent. Les secteurs composés d'une mosaïque d'habitats hétérogènes comme l'archipel du lac Saint-Pierre devraient abriter une communauté de poissons plus diversifiée que celles de secteurs isolés par la présence de barrages comme le lac Saint-François. Les récoltes de deux engins de pêche (c.-à-d. la seine de rivage et le filet maillant) ont été analysées séparément pour prendre en compte le biais relié à la sélectivité : le filet maillant capture des espèces plus larges et plus mobiles dans des habitats plus profonds (1,5-14 m) que la seine de rivage (0-1,5 m). Ce premier chapitre a été abordé avec l'intention d'utiliser un réseau de suivi ichtyologique standardisé (1995-2013), d'identifier les zones ayant une diversité ichtyologique élevée, et de délimiter des unités de gestion qui s'appuient davantage sur une réalité écologique.

Titre du Chapitre II. Les multiples facettes de la connectivité : modélisation des frayères et des nourriceries qui contribuent efficacement au recrutement des jeunes stades de vie dans un fleuve Saint-Laurent dépourvu d'activités humaines.

À plus fine échelle spatiotemporelle, le chapitre II s'intéresse au niveau d'organisation populationnelle. Il vise à étudier l'importance de la connectivité des habitats sur l'efficacité des frayères dans deux régions contrastées du fleuve Saint-Laurent: le tronçon étroit entre Montréal et Sorel (46 km de long) et le lac Saint-Pierre (48 km de long). Le grand brochet (*Esox lucius*), qui exploite des habitats typiques et bien documentés de la plaine d'inondation lors de sa reproduction, est utilisé comme espèce modèle. Ce prédateur de niveau trophique supérieur structure la communauté de poissons. De plus, la population du grand brochet est en déclin depuis le milieu des années 1990 dans le fleuve Saint-Laurent. La modélisation des habitats de nourriceries du grand brochet développée dans cette thèse pour la période 1965-2013 a été couplée à un modèle de fraie existant. Le chapitre II vise ensuite à adapter au milieu aquatique des méthodes d'analyse spatiale des habitats propres aux habitats terrestres, à calibrer les mesures de connectivité entre les frayères et les nourriceries, et à tester la sensibilité de paramètres clés (par ex. la dispersion des larves) au paysage hétérogène du fleuve Saint-Laurent. L'hypothèse qui a été formulée est la suivante : les rapides variations de niveaux d'eau et de courants ont des effets marqués sur la connectivité des habitats. Plus précisément, les variations de niveau d'eau entre le dépôt des œufs dans les frayères et le déplacement des larves du grand brochet vers les nourriceries (pendant 5 semaines), ainsi que la vitesse du courant, sont des facteurs clés qui limitent ou facilitent la connectivité entre les frayères et les nourriceries. Alors qu'on suppose qu'un lac fluvial est sujet à de fortes variations de niveau d'eau qui déconnectent les habitats, le fort courant présent dans un corridor étroit doit disperser les larves vers des habitats non propices. Grâce à la modélisation, les premières mesures de connectivité ont été réalisées dans un paysage vierge, volontairement dépourvu d'activités humaines. Cela a permis de tester l'effet

de trois conditions hydrologiques contrastées (c.-à-d. un niveau d'eau bas et stable, un niveau d'eau qui augmente et un niveau d'eau qui diminue) sur le déplacement des larves à partir des frayères vers les nourriceries. La modélisation du chapitre II a été réalisée dans une plaine d'inondation vierge, c'est à dire volontairement dépourvue d'activités humaines, afin d'éviter les effets confondant liés à la présence de l'homme.

Titre du Chapitre III. Modélisation des frayères effectives du grand brochet au lac Saint-Pierre : une inversion des conditions les plus productives causée par les activités humaines.

Le chapitre III vise à mesurer l'effet de la régularisation du débit et de l'expansion de l'agriculture sur la connectivité et l'efficacité des frayères du grand brochet au lac Saint-Pierre (48 km de long). L'état naturel du lac Saint-Pierre modélisé dans le chapitre II est ainsi comparé à son état contemporain (2014), qui a été transformé par la présence de l'homme. Alors que la régularisation du fleuve Saint-Laurent a profondément transformé le signal naturel du régime hydrologique depuis 1911 en réduisant la durée de l'inondation, on émet l'hypothèse que la connectivité des habitats du lac Saint-Pierre ait été réduite par le régime régularisé. De plus, on s'attend à ce que l'agriculture dans la plaine d'inondation ait fortement détérioré des habitats historiquement productifs pour le grand brochet, surtout depuis la dernière vague d'intensification de l'agriculture des années 1990. Le chapitre III vise à identifier les secteurs les plus productifs pour la reproduction du grand brochet et les plus touchés par les pressions anthropiques pour fournir des éléments concrets pour la restauration et la mise-en-valeur d'une espèce emblématique aujourd'hui en déclin.

Tableau 0.2 Contributions des auteurs ayant participé aux articles composant le corps de cette thèse (AF= Aline Foubert, MC= Mathieu Cusson, FL= Frédéric Lecomte, MM=Marc Mingelbier, PL= Pierre Legendre, CLP= Céline Le Pichon, JM= Jean Morin, JF= John Farrell, PB= Philippe Brodeur)

	I	**II**	**III**
Idée originale	AF, FL, MC, MM	AF, FL, MM	AF, FL, MM
Méthodes (design)	AF, FL, MC, PL	AF, CLP, FL, JF, JM, MM	AF, CLP, FL, MM, PB
Méthodes (réalisation)	AF	AF	AF
Interprétation des résultats	AF, FL, MC, PL	AF, CLP, FL, MM	AF, FL, MM, PB
Rédaction du manuscrit	AF	AF	AF
Relecture	FL, MC, PL	CLP, FL, JF, JM, MM	CLP, FL, MM, PB

CHAPITRE I

SPATIAL ORGANIZATION OF FISH COMMUNITIES IN THE ST. LAWRENCE RIVER: A TEST FOR LONGITUDINAL GRADIENTS AND SPATIAL HETEROGENEITIES IN A LARGE RIVER SYSTEM

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1.1 Abstract

Typified by heterogeneous habitats, large rivers host diversified communities throughout their course. As the spatial organisation of fish communities within these ecosystems remains little studied, longitudinal gradients and spatial heterogeneities of fish diversity were analysed in the large temperate St. Lawrence River, Canada. We used two distinct datasets obtained from either seine nets or gillnets from governmental standardised fish surveys (1995-2012) consisting of a total of 299 662 individuals from 76 fish species captured in 1 051 sites. Results from diversity indices and multivariate analysis revealed a gradual downstream increase in taxonomic diversity, and a gradual change of the community structure along the river. In addition, we observed different fish communities within fluvial lakes and corridors and found significant differences in fish community structure between opposite shores. The fish communities described along the river using seine nets are spatially more heterogeneous than when described using gillnets. This discrepancy is likely

resulting both from the more mobile species targeted by gillnets and sampling sites located farther from the shallower shoreline habitat targeted by seine nets. The organisation of fish communities stresses the need to implement science-based policies and actions to preserve biodiversity and restore communities distributed over large heterogeneous ecosystems.

Keywords: fish diversity, discontinuities, multiscale, riverscape, seine nets, gillnets.

1.2 Introduction

Large rivers are composed of a mosaic of habitats supporting diversified communities of plants and animals. Landscape heterogeneity, as well as environmental conditions and disturbances, are recognized as primary forces shaping the spatial distribution of fish communities (Robinson *et al*. 2002; Ward *et al*. 2002; Nilsson *et al*. 2005). Albeit widely studied in streams and small to medium-size rivers (Pekárik *et al*. 2011; Suvarnaraksha *et al*. 2012; Konan *et al*. 2015), only a few large rivers were studied over extensive stretch (e.g. Missouri, Galat *et al*. 2005; Gange, Das *et al*. 2013; Mekong, Chea *et al*. 2016) perhaps due to the sheer size of those systems and the lack of large scale standardised surveys. Large rivers are distinguished from medium-sized rivers as the former's mean annual discharge exceed 7 500 $m^3.s^{-1}$ and their watershed is larger than 900 000 km^2 (Bethemont 2003).

In past years, several theoretical concepts focusing on communities organisation along entire river systems were proposed (reviewed in Johnson et Host 2010; Melles *et al*. 2012; Ellis et Jones 2013). For example, the River Continuum Concept (RCC; Vannote *et al*. 1980) describes rivers as a longitudinal gradient of environmental conditions shaping the distribution and organisation of communities from the headwater to the river mouth (e.g. Naiman *et al*. 1987; Jiang *et al*. 2011; Wolff *et al*. 2013). In parallel, the Serial Discontinuity Concept (SDC; Ward et Stanford 1983; Ward et Stanford 1995) predicts that natural and anthropogenic disruptions will lead

to longitudinal discontinuities in biological organisation at the population level (e.g. abundance), community (e.g. richness, dominance) or even at the ecosystem level (e.g. productivity). The SDC is a conceptual framework often used to explain the effects of dams, tributaries or geomorphological discontinuities on biological organisation in the river continuum (Hillbricht-Ilkowska 1999; Stanford et Ward 2001; Kiffney *et al*. 2006).

Considering the river as a single flowing channel, both RCC and SDC do not offer a complete perspective on the spatial heterogeneity of fish organization in large river systems (e.g. Sedell *et al*. 1989; Johnson *et al*. 1995; Dettmers *et al*. 2001; Araùjo *et al*. 2009). On the other hand, integrative theoretical concepts with a broader framework were developed (e.g. Riverscape and River Wave Concept, Poole 2002; Humphries *et al*. 2014). For example, the concept of Riverscape (Fausch *et al*. 2002; Poole 2002; Wiens 2002), which recognized the importance of continuous, hierarchical and heterogeneous properties of the river, integrates longitudinal gradients and discontinuities within a spatially explicit framework (e.g. Le Pichon *et al*. 2017). This concept assumes that while geomorphologically-distinct entities (e.g. fluvial lakes, rapids, channellized areas, etc.) observed along a riverscape (i.e. between 1-100 km, Fausch *et al*. 2002) are ecologically connected along the upstream-downstream axis, they nevertheless possess unique biologial caracteristics owing to local spatial heterogeneity (importance of uniqueness, Poole 2002). Considering the overall heterogeneity of the entire river (i.e. longitudinal, lateral and vertical patterns) at different spatial scales, the riverscape concept may ultimately help explaining the complex biotic community patterns observed in large rivers (e.g. Frenette *et al*. 2012; Massicotte *et al*. 2014; Gladyshev *et al*. 2015).

The main objective of this study was to assess the spatial organisation of fish communities in a large temperate river across multiple spatial scales. Specifically, we (1) characterised the fish diversity along the longitudinal upstream-downstream axis

of the St. Lawrence River (Québec, Canada), (2) identified potential longitudinal discontinuities along north and south shores and (3) assessed relationships between riverscape heterogeneity and fish communities at i) hydro-morphological (fluvial lakes vs. corridors), ii) sector, and iii) shore scales. To fulfil these objectives, we analysed the fish community structure using a large data set covering the St. Lawrence River from Cornwall to Québec City (424 km stretch). The portion studied is highly heterogeneous both longitudinally and transversally (i.e. between opposing shores) due to the hydro-morphological characteristics of water bodies. We predicted that species distribution along the St. Lawrence River is associated with the longitudinal series of fluvial lakes alternating with narrow corridors, rapids, archipelagos, and the presence of a freshwater tidal zone in the downstream portion. Moreover, as the deep navigational channel is dividing the river in a northern and southern portion all along its course, we expected that fish communities are structured differently along each shore.

1.3 Methods

1.3.1 Study area

The St. Lawrence River is one of the largest rivers in the world, both in terms of watershed area (1 344 200 km^2) and mean annual discharge (12,600 $m^3.s^{-1}$ at Québec city; Morin et Bouchard 2000). The St. Lawrence River drains the North American Great Lakes, which contains more than 20% of all freshwater reserves of the world to the Gulf of St.Lawrence which is connected to the Atlantic Ocean. The 550 km freshwater portion of the river, from the lake Ontario outlet to Québec City (Figure 1.1), is generally shallow (<3 m) except for an artificially maintained navigation channel that divides the river transversally (the St. Lawrence Seaway; width ≥300 m; depth ≥11.3 m downstream Montréal harbour and ≥8.2 m upstream Montréal; mean current velocity of 0.5-2.0 $m•s^{-1}$). Most of water flow occurs in the navigation channel (up to 90%) and no water exchanges occur between the north and south shores.

Indeed, three main water masses are flowing side-by-side without mixing in the portion upstream of Trois-Rivières (Frenette *et al*. 2006; Hudon et Carignan 2008). Downstream of this area, mixing occurs as the influence of tides increases and even tidal flow reversal is noticeable downstream of Donnacona (Figure 1.1, Centre-Saint-Laurent 1998). The uninterrupted freshwater river section (350 km) of the St. Lawrence River spans from the Beauharnois Dam downstream to the middle estuary where it continues uninterrupted to the sea (Figure 1.1). In our study site, only Lake Saint-François is located upstream of the Beauharnois Dam and downstream of the Moses-Saunders Dam. Lake Saint-François water level is fully stabilised and its water flow regulated by the two dams operated for hydroelectric power production (Morin *et al*. 2000; La Violette 2004).

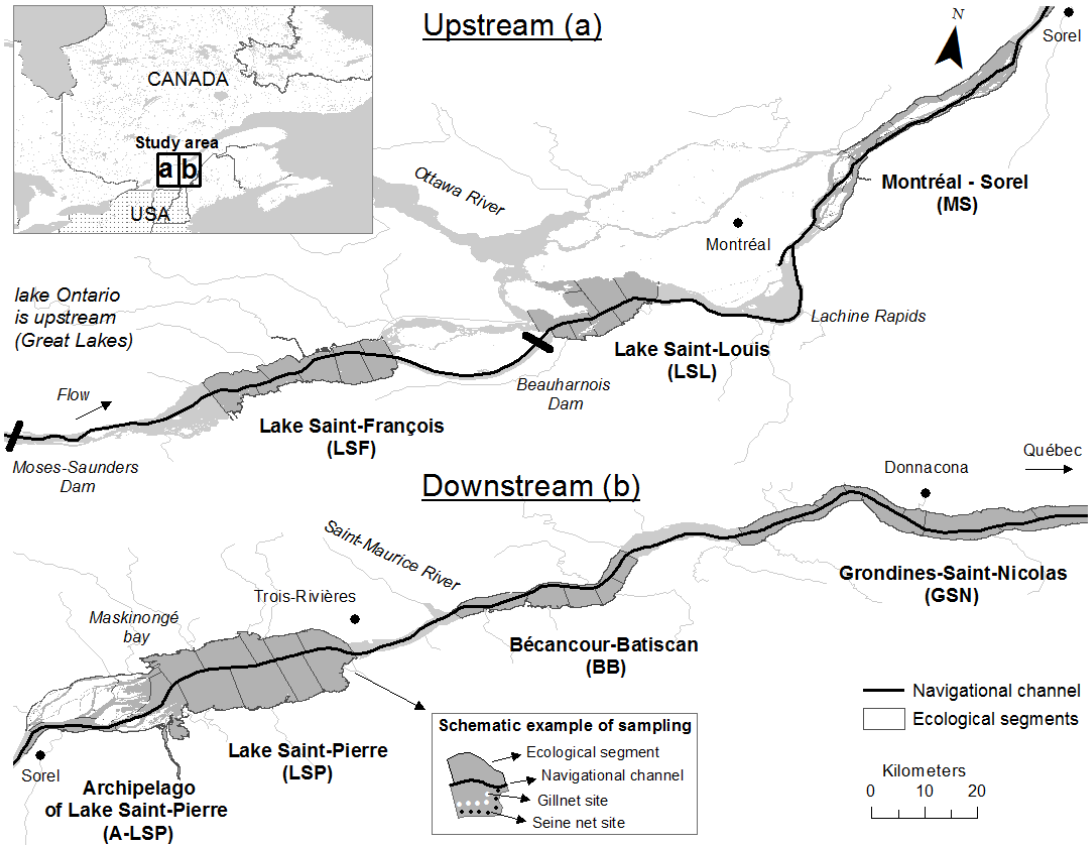

Figure 1.1 Map of the sectors studied (LSF, LSL, MS, A-LSP, LSP, BB and GSN) along the St. Lawrence River. The ecological segments and the navigation channel separating the shores are also shown. Note that for clarity the map was cut into two portions (upstream, upper part and downstream, lower part).

A total of 97 freshwater and diadromous fish species, including 9 non-native species, are known to exploit the St. Lawrence River (Ministère de la Faune, des Forêts et des Parcs du Québec data bases). Compared to similar large temperate rivers, fish richness in the St. Lawrence River is relatively high and comparable to Mississippi River (102 species), while it is more diversified than Volga (63 species) or Danube (58 species; Galat et Zweimüller 2001 and the references therein). The high diversity observed in the St. Lawrence River may result from the combination of the inland post-glacial recolonization routes following the Wisconsinan glaciation to the natural connectivity with the Atlantic coast through the Gulf of St. Lawrence (Legendre et Legendre 1984; Lacasse et Magnan 1994).

1.3.2 The standardized fish survey

The standardised governmental fish survey in the St. Lawrence River, known as the RSI ("Réseau de Suivi Ichtyologique", described in La Violette *et al*. 2003), characterizes the fish community structure at the end of the growing season (August to October). Due to such late sampling, and the sampling gear employed, only relatively large juvenile (>50 mm) to adult were captured. The whole river is divided in seven different areas (hereafter called sectors) according to their specific hydrological and morphometric characteristics. We thus recognise (Figure 1.1) three distinct fluvial lakes; (1) Lake Saint-François (LSF; width: 7 km, length: 27 km), (2) Lake Saint-Louis (LSL; width: 11 km, length: 18.5 km), and (3) Lake Saint-Pierre (LSP; width: 12.8 km, length: 25.6 km), (4) an archipelago called Lake Saint-Pierre Archipelago (A-LSP; width: 10.5 km, length: 22.4 km) and three narrower corridor sections including (5) Montréal-Sorel (MS; width: 3 km, length: 46 km), (6) Bécancour-Batiscan (BB; width: 3 km, length: 28 km), and (7) Grondines-Saint-Nicolas (GSN; width: 3 km, length: 55 km). Numbers were added to sector acronyms to ease locate them along the upstream / downstream axis of the river (Figure 1.1). The fluvial lakes observed along the St.Lawrence river are natural (e.g. not manmade). Although seemingly analogous to pools observed along a stream gradient,

they are functionally dissimilar since fluvial lakes are not associated with the presence of deeper portions of the river (i.e. pools) but rather created by water flowing over shallower areas combined with an enlargement of the main tributary. Although Lake Saint-François increased in size after damming the river, it did exist prior to the construction of the Beauharnois Dam. While the last two sectors are contiguous (6-BB and 7-GSN), they are considered separately as Grondines marks the beginning of mesotidal portion of the fluvial estuary with average tidal amplitude of 1.8 m (Gauthier 2000). The Lachine Rapids, south of Montréal, were not considered in the present study because the powerful hydrodynamic flow regime prevents the use of the standardised sampling surveys protocol.

Fish communities were sampled approximately every one km of shoreline: such sampling scheme was determined as a trade-off between sampling effort vs. area covered while allowing enough statistical power to detect significant spatial changes in the community structure (Flotemersch *et al*. 2011). A multiple-gear approach was implemented in the RSI as it is considered the most efficient approach to assess fish community organisation in large heterogeneous rivers (Galat *et al*. 2005; De Leeuw *et al*. 2007). The RSI uses (1) a standardised beach seine net (12.5 m long × 4 m deep and 3.2 mm stretched mesh) and (2) an array of two multimesh gillnets (60 m long × 1.8 m deep; eight panels of 25, 38, 51, 64, 76, 102, 127 and 152 mm stretched mesh, 15-28.5 hours fishing period; La Violette *et al*. 2003). Seine nets were preferred for sampling the fish community in lentic and nearshore littoral habitats (depth <1.5 m), while gillnets were used for sampling lentic and lotic midshore littoral habitats in the deeper water column adjacent to the seine (depth between 1.5 and 14 m; average of 6.2 m; Figure 1.1). Two distinct gears were analysed separately to take into account bias related to selectivity and the specific habitats sampled. Gillnets captured larger and more mobile fishes in a deeper water column located farther from the shallower shoreline habitat targeted by seine nets (La Violette 2004). Both gears have been shown to be efficient in assessing fish community diversity in rivers and detecting

changes in fish community structure (Leclerc 1990; Argent et Kimmel 2005; Ri et Gelwick 2005; Lapointe *et al*. 2006).

Due to the sheer size of the St. Lawrence River, only one or two sectors were sampled yearly. From 1995 to 2012, all sectors were sampled three times, except for 3-MS, 7-GSN and 6-BB that were sampled one, two and four times respectively. As we intend to focus on spatial patterns in the present study, we analysed the interaction between the space and time factors to ensure that sites sampled from different years can be pooled into their sectors/segments (defined below). The space-time interaction method (STI) allows testing space–time interaction in repeated ecological survey data, when there is no replication at the level of individual sampling sites (Legendre *et al.* 2010). A significant interaction would indicate that the spatial structure of the communities has changed between surveys, so that survey results could not be pooled. Due to the RSI sampling design, STI was performed on the five sectors that have been sampled tree times (1-LSF, 2-LSL, 4-A-LSP, 5-LSP, 6-BB) at the sector and segment scales, for both the seine and gillnet gears. None of the analysis showed significant space-time interaction. Since the spatial structure of the fish communities did not change significantly between the RSI sampling periods for both gears, we pooled the site samples from different years into their sectors/segments to better represent the "average" local community structure.

When considering both gears, a total of 1 051 sites were sampled one to four times over the 17 years period (total of 2 386 samples; appendix Table A.1). A grand total of 519 sites were sampled using seine nets (total of 1 127 samples) and 532 sites were sampled using gillnets (total of 1 259 samples). In each sector, an average (± SD) of 74 (± 34) sites were sampled with seine nets and 76 (± 12) with gillnets. While considering seine net and gillnet samples separately, sites were grouped within ecological segment (named hereafter segment) predefined by the ecological reference framework from the present Ministère du Développement Durable, de

l'Environnement et de la Lutte contre les Changements Climatiques du Québec (DesGranges et Ducruc 1998). The ecological segments were defined by the general shoreline morphology (i.e. based on 25 specific shapes such as straight, sinuous, indented, "closed" or "open" bay) observed by satellite imagery, aerial photography (see Figure 1.1) and various geomorphologic features describing the physical landscape both below and above water (e.g. sandy vs. rocky shores, presence of cliffs, water velocity, urbanisation, occupation of the coastline, extent of floodplain/intertidal zone, etc). Finally, as the deep navigational channel is dividing the river in a northern and southern portion along its entire course, it was possible to analyse each shore separately for either seine and gillnet samples. As such, individual segment includes samples collected along only one shore. The average number of sites per segment was 19 (± 9) and 20 (± 12) for the seine and gillnet respectively. Along the entire study area, a total of 63 segments were defined with an average of 9 (± 1) segments per sector (Figure 1.1; appendix Table A.1).

1.3.3 Indices of diversity

Fish diversity was analysed using three complementary and robust indices. Firstly, the rarefaction index (ES_n) of Hurlbert (1971) corresponds to the expected number of species identified from a random subsample; the subsample size was set to 70 individuals for the seine (ES_{70}) and 30 individuals for the gillnet (ES_{30}). The rarefaction index allows the comparison of species richness from unequal sampling effort. A minimum of (*n*) 30 individuals is usually required for a good estimate of the rarefaction index (Gotelli et Colwell 2001). This criterion was not met for only one segment sampled using gillnet located in the Montréal-Sorel sector. Secondly, we calculated from the raw data the Simpson diversity (1-λ') that takes into account both species richness and abundance distribution. Thirdly, we used the average taxonomic distinctness (Δ*, that is the expected taxonomic distance to the order level apart from two individuals from different species chosen at random from the sample) to estimate

the taxonomic "breadth" of an assemblage and the relatedness of its constituent species (Clarke et Warwick 1998).

1.3.4 Data analysis

All analyses targeting fish communities sampled by either seine of gillnet were always analysed separately. The smallest statistical unit is represented by the ecological segments rather than sampling sites (i.e. unit of analyses); all samples collected within an individual ecological segment were pooled without regard to the sampling year. We used a hierarchical subset design to test differences among (i) opposing shores within sectors (north vs. south shores); (ii) sectors (1-LSF, 2-LSL, 3-MS, 4-A-LSP, 5-LSP, 6-BB, 7-GSN), and (iii) hydro-morphological scale (fluvial lakes vs. corridor vs. archipelago).

1.3.4.1 Longitudinal gradients

Differences in diversity indices among the fixed factors of sectors were tested, one at a time, using a non-parametric permutational multivariate analysis of variance (PERMANOVA, with 9999 permutations; Anderson *et al*. 2008) with Euclidian distance matrix. PERMANOVA generates the null distribution of the test statistic without assumptions of normality (Fairclough *et al*. 2008). Moreover, the gradual downstream increased in diversity indices (i.e. rarefaction index, Simpson diversity and average taxonomic distinctness) was tested using the non-parametric Spearman correlation coefficient (Zar 1972). As we believe that 7-GSN specificities (e.g. beginning of mesotidal portion of the fluvial estuary) may impede detecting such diversity patterns, Spearman correlations were also performed excluding this most downstream sector.

A multivariate seriation test (Index of Multivariate Seriation IMS; RELATE procedure with maximum 999 permutations with Bray-Curtis dissimilarities, segments oriented upstream-downstream were compared for each shore separately)

was used to determine if fish community structure changes gradually along the longitudinal axis of the river (Somerfield *et al*. 2002; Clarke *et al*. 2014). Abundance data were log transformed to adjust the balance between the contributions of dominant and rarer species (Clarke 1993) and were separately analysed along the north and south shores. If community changes along the St. Lawrence River conform to a stepping-stone model of variation (e.g. segment one is more similar to its neighbouring segments than distant segments while the amplitude of dissimilarity is correlated with distance), the correlation will be maximized and the index, IMS (Rho), would equal the highest value (=1). The seriations were separately analysed for two types of gears and shores. IMS results were visualised using nonmetric multidimensional scaling plot (nMDS plot).

1.3.4.2 Longitudinal discontinuities

As data can be listed as a spatial sequence, the contiguity information can be used to identify discontinuities along the series (De'ath et Fabricius 2000; Borcard *et al*. 2011). A multivariate regression tree (MRT) was used to identify discontinuities along the upstream-downstream gradient of north and south shores of St. Lawrence River using log-transformed species abundance. The result is a tree whose "leaves" (terminal groups of segments) are made up of subsets of segments, which minimize the within-group sums of squares.

1.3.4.3 Spatial heterogeneities

Differences among fish community structure (log-transformed abundance, Bray-Curtis similarities) among the fixed factors of i) opposing shores withing sectors (north vs. south), ii) sectors, and iii) hydro-morphological units (fluvial lakes vs. corridors vs. archipelago) were investigated using PERMANOVA with 9999 permutations. Due to small number of permutations for all treatments when comparing shores within sector, Monte Carlo *P*-values (pmc) were used (Anderson *et al.* 2008).

Community structure discriminated according to the abovementioned factors was compared using a Principal Coordinate Analysis (PCoA; Anderson *et al.* 2008) that represents the distance between every pair of segments in a 2 dimentional array (only axis 1 and 2 were considered). The later was combined to an Indicator Species Analysis (IndVal; Dufrene et Legendre 1997) that identify species significantly associated to the various factors considered in the PCoA (e.g. considering only the north shore sampled using a seine, what are the species significantly associated to lakes vs. corridors vs. archipelago?). As the IndVal can identify indicative species only for dichotomous contrasts (e.g. lakes vs. corridors), the presence of the third category in the form of the archipelago (4-A-LSP) requires the IndVal to be coupled to a multi-levels pattern analysis (e.g. De Cáceres *et al.* 2010; Casatti *et al.* 2012). Significance was tested using a random permutation procedure (Dufrene et Legendre 1997). IndVal analysis were also performed to identify indicator species in each seven sectors (1-LSF, 2-LSL, 3-MS, 4-A-LSP, 5-LSP, 6-BB, 7-GSN), in each hydro-morphological units and to contrast the fish community sampled by seine and gillnet at river scale.

All analysis were performed using PRIMER-PERMANOVA (version 6.1, Plymouth Marine Laboratory; Clarke et Gorley 2006) and R functions (version 3.1.3; R Core Team 2015) with *mvpart* function for the MRT analysis and *multipatt* function for the IndVal analysis. A significant level of $\alpha = 0.05$ was used for all statistical tests. The "Holm" adjustment method (Holm 1979) was used to correct the significance level when multiple comparison were done (with p.adjust function in R, De Cáceres *et al*. 2010).

1.4 Results

1.4.1 Fish communities collected

The entire data set encompassed a total of 299 662 individual fish belonging to 76 species and 25 families (appendix Table A.2). A total of 249 309 fish were

captured by seine nets in nearshore littoral habitats (<1.5 m), while 50 353 fish were captured by gillnets in midshore littoral habitats (>1.5 m). The two gears captured different array of species in all sectors of the St. Lawrence River (PERMANOVA, P <0.001); the seine collected 71 species belonging to 24 families while the gillnet captured 45 species belonging to 20 families. The number of species observed per sample varied from 0 to 26 species (mean ± SD: 8.3 ± 4.6) for seine sites and 0 to 18 species (6.4 ± 2.8) for gillnet sites. As revealed by the IndVal analyses, the community captured by seine was composed of 27 indicator species, including several Cyprinids, whereas 10 species, including larger and more mobile fishes, such as *Acipenser fulvescens* and *Lota lota*, characterised the community captured by gillnet (appendix Table A.3).

1.4.2 Longitudinal gradients

1.4.2.1 Diversity indices

From upstream to downstream, the total number of species changed from 46 species in 1-LSF, 58 in 2-LSL, 52 in 3-MS, 55 in 4-A-LSP, 56 in 5-LSP, 56 in 6-BB and finally 37 in 7-GSN. In 1-LSF, all diversity indices for both seine and gillnet were low (Figure 1.2). Conversely, except for the average taxonomic distinctness for community collected by seine (Figure 1.2e), the 4-A-LSP exhibited high values of diversity. Illustrating the complementarity of information brought by the various indices, despite the fact that 7-GSN showed high average taxonomic distinctness values for both gears (Figure 1.2e, f), 7-GSN had lower values for rarefaction indices (i.e. expected richness for ES70 and ES30, see methods) and Simpson diversity (1 λ'). The 2-LSL community captured by seine exhibited high values of rarefaction and Simpson indices (Figure 1.2a, c) but not the community captured by gillnet (Figure 1.2b, d). For both gears, 6-BB exhibited high values of three diversity indices while 5-LSP and 3-MS showed intermediate values. Only the average taxonomic distinctness values in successive sectors gradually increase from the headwater to the

river mouth for the communities captured by seine (Spearman correlation coefficient of 0.86, P =0.01, Figure 1.2e). However, when excluding 7-GSN that marks the beginning of mesotidal portion of the fluvial estuary, the rarefaction index (Spearman correlation coefficient of 0.94, P =0.008), the Simpson diversity (Spearman correlation coefficient of 0.83, P =0.02) and the average taxonomic distinctness (Spearman correlation coefficient of 0.77, P =0.05) also gradually increase downstream for communities captured by gillnet (Figure 1.2b, d, f). Conversely, even when 7-GSN was excluded, the rarefaction index and Simpson diversity for communities captured by seine still do not support a significant downstream increase (Figure 1.2a, c).

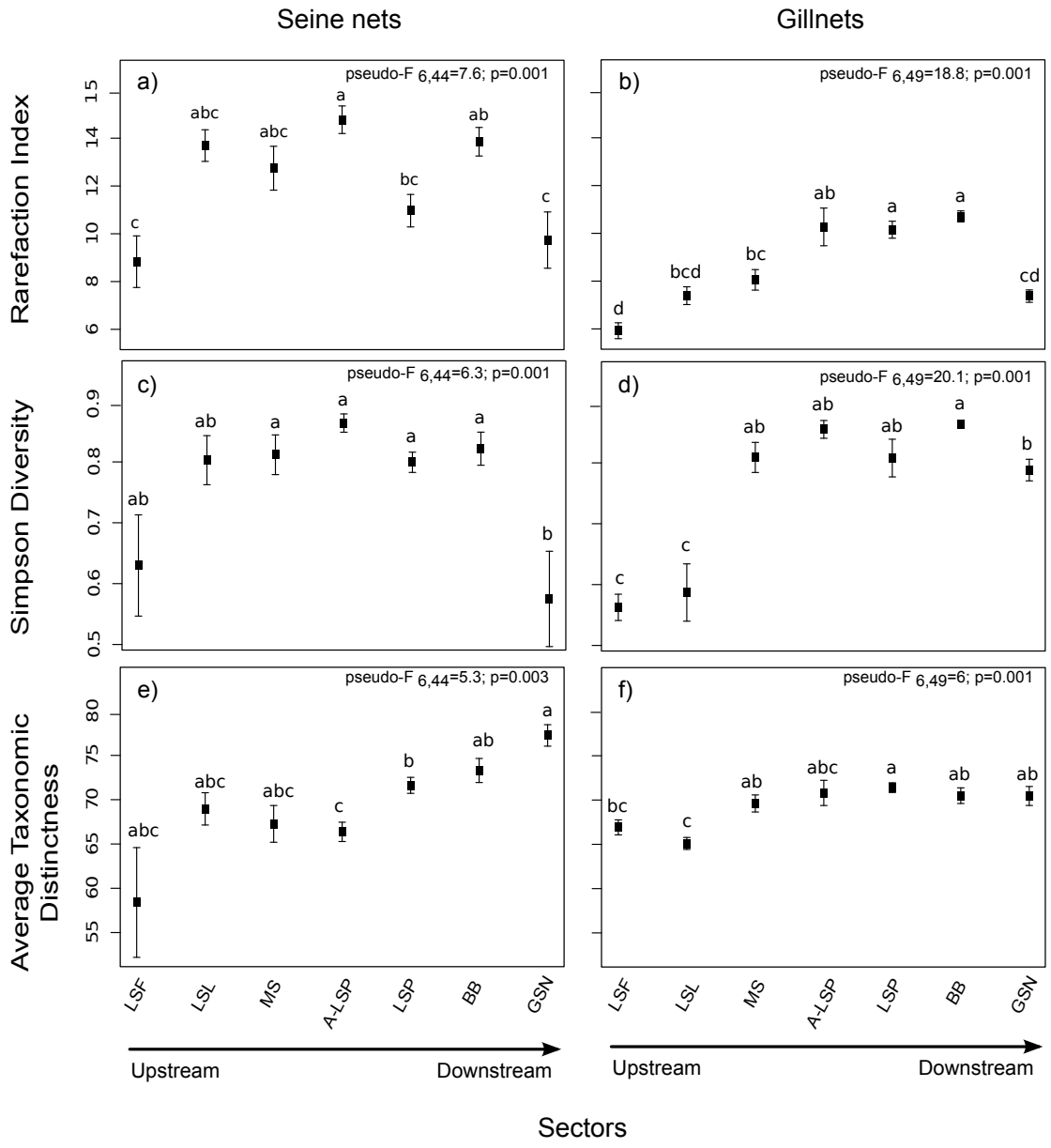

Figure 1.2 Point bars showing average values (± SE) of rarefaction index (ES_{30} and ES_{70} for gillnets and seine nets respectively, see methods), Simpson diversity and taxonomic distinctness among sectors of the St. Lawrence River for fish communities collected by seine nets (graphs a, c, e) and gillnets (graphs b, d, f). Sectors were ordered from upstream (left) to downstream (right). Different letters above bars represent significant differences (P <0.05).

1.4.2.2 IMS results

Results from the index of multivariate seriation (IMS) analysis revealed that fish communities gradually changed along the St. Lawrence River with a significant IMS trend (P <0.007; appendix Figure A.2). Rho values indicating the strength of a gradual change along the upstream-downstream axis, were higher for gillnet (0.59) than for seine (0.48) and higher for north shore (0.64 for both seine and gillnet) than for south shore communities (0.43 for seine and 0.56 for gillnet).

1.4.3 Longitudinal discontinuities

The multivariate regression trees (MRT; Figure 1.3 and Figure 1.4) highlighted the elevated disparities between sectors along the river, such as between the 1-LSF and the 2-LSL separated by a dam. Furthermore, the precision of the MRT analysis even suggest that the St. Lawrence River may be subdivided differently depending on the gear considered compared to the actual generalisation of the dichotomous lake vs. corridor sectors (Figure 1.3). For example, the MRT identify a major break in the community captured by seine of northern 5-LSP while such break is inexistent for the community captured by gillnet (Figure 1.4). On the other hand, different sectors appeared undifferentiated for some community such as the northern community of the 5-LSP captured by seine that stretches downstream into the 6-BB sector (Figure 1.3).

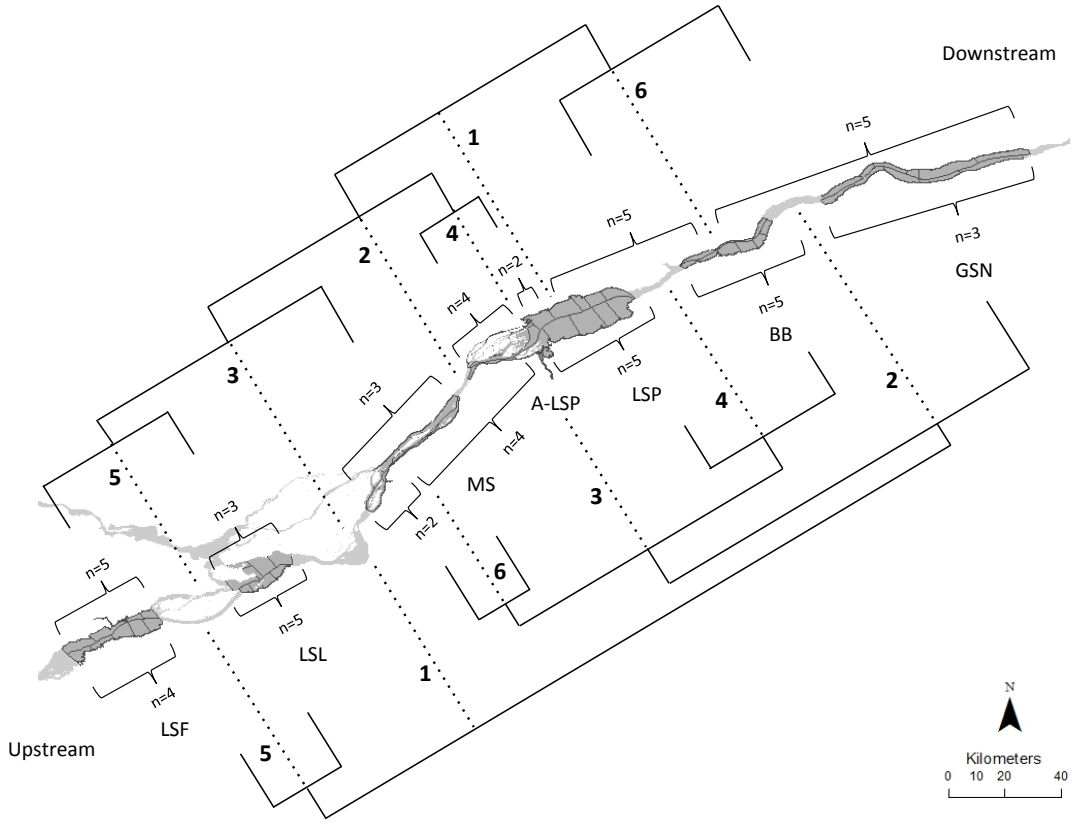

Figure 1.3 Discontinuities (dotted line) in fish communities captured by seine nets (with their node numbers) identified along the St. Lawrence River using a multivariate regression tree analysis (MRT). The navigation channel is used to separate the north from the south shore. For each leaf, the number of segments pooled is indicated. The tree explained 66% and 61.8% of the total sum of squares for the north and south shore respectively.

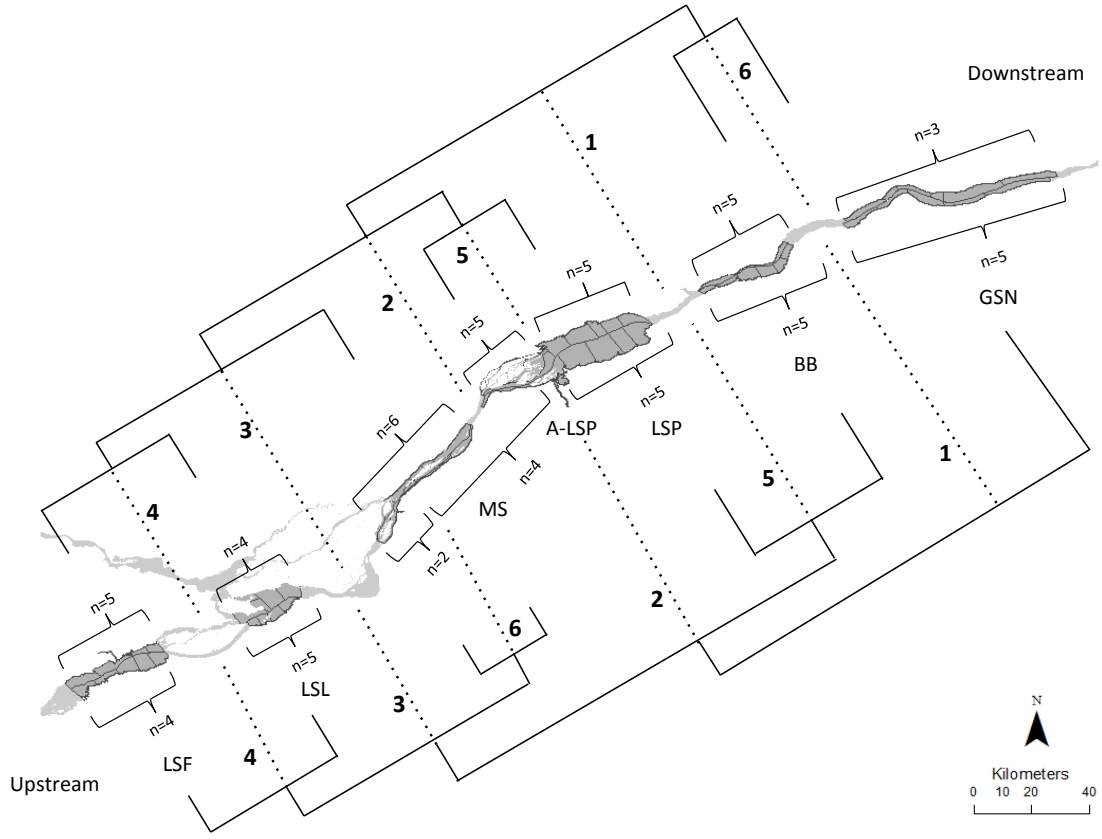

Figure 1.4 Discontinuities in fish communities captured by gillnets identified using a multivariate regression tree analysis (MRT): see legend of Figure 1.3. The tree explained 70.4% and 76.2% of the total sum of squares for the north and south shore respectively.

1.4.4 Spatial heterogeneities

1.4.4.1 Differences between hydro-morphological units

Fluvial lakes (1-LSF, 2-LSL and 5-LSP), corridors (3-MS, 6-BB and 7-GSN) and the archipelago (4-A-LSP) are home to different fish communities. There were significant differences between hydro-morphological units for the community structure sampled using either seine (PERMANOVA; Pseudo-$F_{2;\ 55}$ =8.2; all P <0.004) or gillnet (Pseudo-$F_{2;\ 60}$ =10.6; all P <0.02). These differences were also identified in the PCoA ordination plots (Figure 1.5).

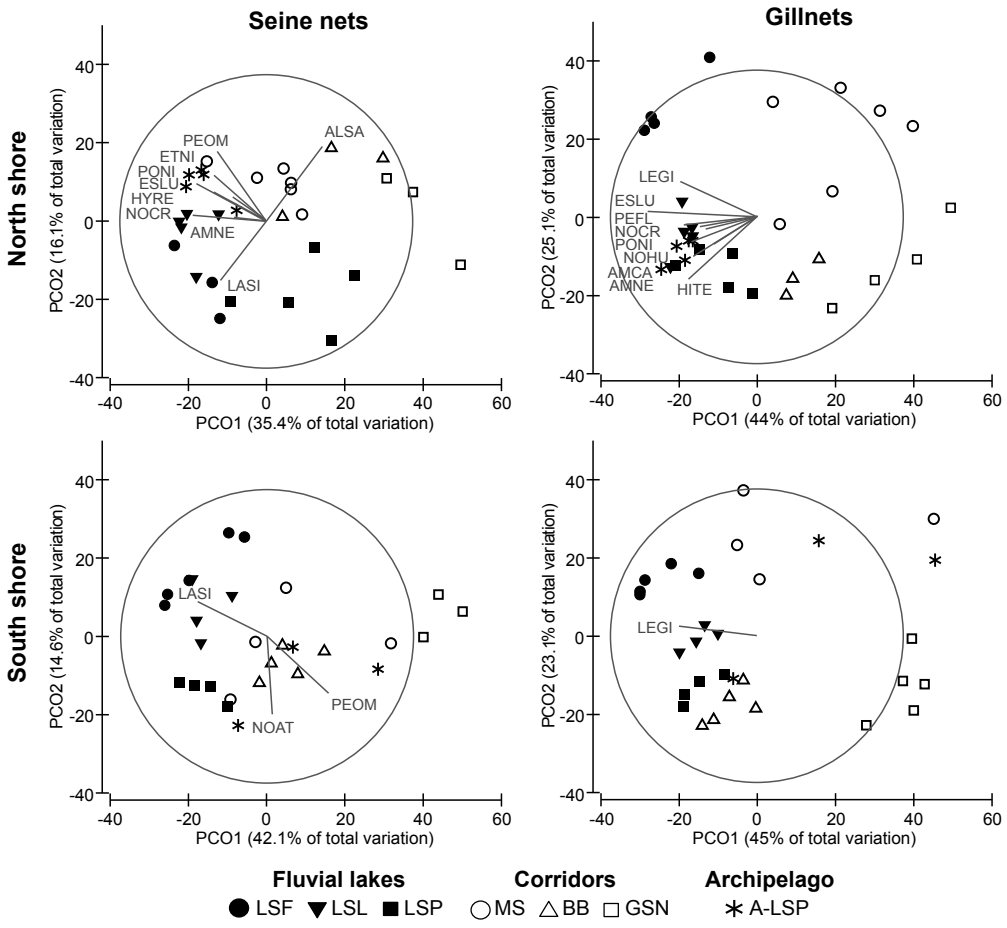

Figure 1.5 Principal Coordinate Analysis (PCoA) plots showing fish communities captured by seine nets (a, c) and gillnets (b, d) at the segment scale

among sectors and shores. Indicator species abbreviations, that characterize fluvial lakes (black symbols), corridors (white symbols) and the archipelago (stars), are as follows: ALSA = *Alosa sapidissima*; AMCA = *Amia calva*; AMNE = *Ameiurus nebulosus*; ESLU = *Esox lucius*; ETNI = *Etheostoma nigrum*; HITE = *Hiodon tergisus*; HYRE = *Hybognathus regius*; LASI = *Labidesthes sicculus*; LEGI = *Lepomis gibbosus*; NOAT = *Notropis atherinoides*; NOCR = *Notemigonus crysoleucas*; NOHU = *Notropis hudsonius*; PEFL = *Perca flavescens*; PEOM = *Percopsis omiscomaycus*; PONI = *Pomoxis nigromaculatus*. The circle is a unit circle (radius =1.0), whose position of origin (centre) corresponds to the centre of the plot (0,0). Each vector begins at the centre of the circle and ends at the coordinates (x, y) consisting of the Pearson correlations between indicator species and each of PCO axis 1 and 2, respectively. The length and direction of each vector indicates the strength and sign, respectively, of the relationship between indicator species and the PCO axes.

In fluvial lakes, four indicator species were identified using IndVal analysis for the community captured by seine (e.g. *Ameiurus nebulosus* and *Notemigonus crysoleucas*) and seven for the community captured by gillnet (e.g. *Perca flavescens* and *Lepomis gibbosus*). In corridors, four species were also indicators of the seine (e.g. *Alosa sapidissima* and *Percopsis omiscomaycus*) while none were found for gillnet (Figure 1.5). In the archipelago, 11 and 9 indicator species were identified for the seine and the gillnet respectively. The smaller number of segments (n=8) present in the archipelago as likely biased upward the number of indicator species detected for this unique sector. A total of 13 of the combined 21 indicator species identified for the archipelago were common with either the fluvial lakes (9) or the corridors (4).

The Bray-Curtis dissimilarity comparisons show that, for both gears, corridor segments are structurally more variable than fluvial lake segments (Figure 1.6). This observation is supported by both (1) the non-overlapping confidence intervals

between lakes and corridors and (2) the higher total variance of Bray-Curtis distances observed for the corridors segments (Figure 1.6). The variability observed within the archipelago is difficult to judge, as only a few segments were available to calculate Bray-Curtis distances.

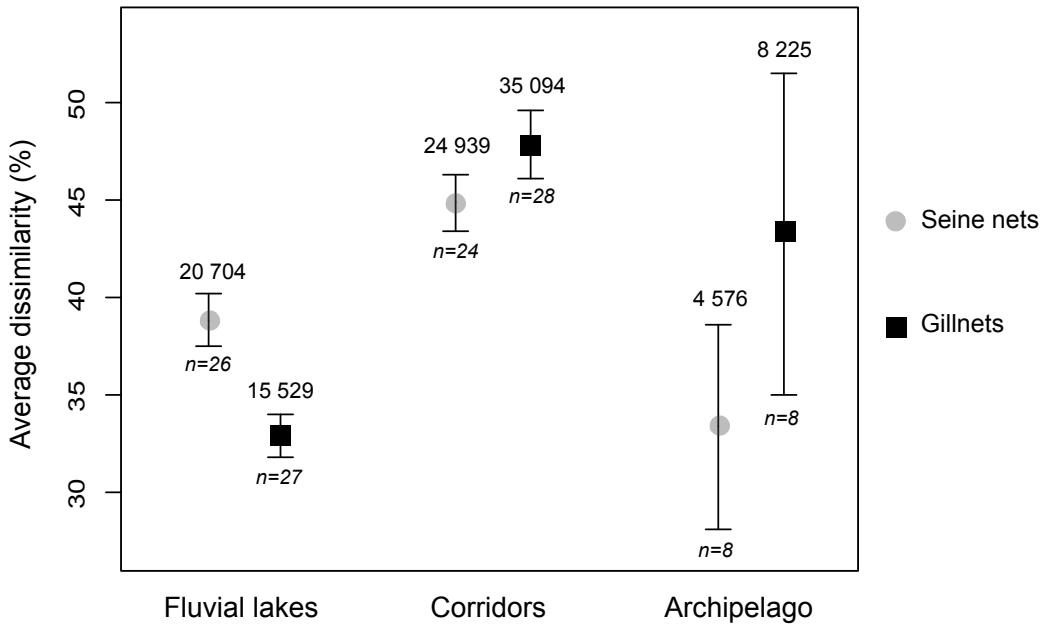

Figure 1.6 Point bars showing average values (± CI 95%) of Bray-Curtis dissimilarity between the seine nets and gillnets for the fluvial lakes, the corridors and the archipelago of the St. Lawrence River. Numbers on the top correspond to the total variance of Bray-Curtis distances and numbers under the bar correspond to the total number of segments.

1.4.4.2 Differences among sectors

For both gears analysed separately, almost every sector hosted significantly distinct fish communities (PERMANOVA, all pairwise P <0.05), the only pairwise comparisons not significant were all from the gillnets database (4-A-LSP vs. 2-LSL, 4-A-LSP vs. 5-LSP, 4-A-LSP vs. 6-BB where P =0.06, P =0.06 and P =0.1

respectively), while 7-GSN appears as the most divergent sector (appendix Table A.4). This latter result reinforces the observation that the St. Lawrence is highly heterogeneous at the sector scale.

Some species are indicators of only one sector such as *Notropis stramineus* in 1-LSF and *Apeltes quadracus* in 6-BB for communities captured by seine (see complete results in appendix Table A.5). In contrast, some species were more common across all sectors with one exception. For example, *Lepomis gibbosus*, *Notemigonus crysoleucas* and *Perca flavescens* were common in all sectors except in 7-GSN for communities captured by seine (appendix Table A.5). Although marine/estuarine species such as *Microgadus tomcod*, *Acipenser oxyrinchus* and *Morone saxatilis* were observed in the 7-GSN sector (appendix Table A.2) and contribute to boost the taxonomic diversity index, they were not recognized as significant indicator species when using the IndVal analysis.

1.4.4.3 Differences between shores

The structure of fish communities was significantly different between north and south shores in 2-LSL, 5-LSP and 6-BB sectors for the communities collected by seine and in 4-A-LSP, 5-LSP and 6-BB for gillnet (PERMANOVA, all P_{mc} <0.05).

Different indicator species were identified in north and south shores. For example, in community captured by seine, *Cyprinella spiloptera* was identified as an indicator species along the north shore whereas *Notropis rubellus* was identified along the south shore of the 2-LSL (see complete results in appendix Table A.6).

1.5 Discussion

The spatial organisation of St. Lawrence fish communities reflects the influence of the river heterogeneity on ecological processes at different spatial scales. It appeared that despite longitudinal gradients, a more complexe and patchy patterns are defining

the spatial organisation of the St. Lawrence River fish communities. The combination of complementary univariate and multivariate analysis of community characteristics greatly improved our ability to detect diversity patterns in a highly heterogeneous ecosystem (Clarke *et al*. 2014). The present study stresses the importance of analysing global patterns of diversity using robust diversity indices to avoid biasing estimates resulting from gears used and sampling effort (Gotelli et Colwell 2001) and to go beyond the overly simplistic view provided by considering the total number of species as an index describing the organisation of fish communities. Moreover, the sensitivity of the various univariate diversity indices (e.g. specific vs. taxonomic indices) had to be considered toward their relevance in covering general assembly rules such as ecological gradients.

1.5.1 Longitudinal patterns

The results revealed the presence of a longitudinal component (i.e. upstream-downstream axis) of fish cummunities organisation along the St. Lawrence River; diversified sectors are not only the result of their intrinsic properties but also the result of their position along the continuum. More generally, the longitudinal pattern along the St. Lawrence River appears as a combination of (1) the decreasing anthropogenic habitat alterations from the headwater toward the river mouth and (2) the riverscape heterogeneity along the continuum (e.g. hydro-morphological changes), which increase the dissimilarity between upstream and downstream fish communities and contribute to the gradual increase in taxonomic diversity.

Firstly, as predicted by the Serial Discontinuity Concept, the reduced specific and taxonomic fish diversity in the upstream Lake Saint-François (1-LSF) and the distinct communities observed in the adjacent sector of Lake Saint-Louis (2-LSL) reflect the impacts of the physical isolation of the 1-LSF created by the Moses-Saunders and the Beauharnois dams. It is clear that dams located on both sides of the 1-LSF have created a distinct water body characterized by altered connectivity, stabilized water

level and increased current velocity that most likely impacted the fish communities, including a reduced number of species (La Violette *et al.* 2003). In many rivers, including large systems, biodiversity observed close to dams is lower than downstream (Stanford et Ward 2001; Nilsson *et al.* 2005; Santos *et al.* 2013; Holt *et al.* 2015). Downstream of Beauharnois dam, the hydrology gradually loss the imprints of upstream water level regulation (Vincent et Dodson 1999).

Secondly, the complex mosaic of habitats in the archipelagos (i.e. Boucherville archipelago in the upper part of 3-MS and 4-A-LSP) increases the specific diversity in the middle part of the St. Lawrence River. The 4-A-LSP hosts the richest (in rarefaction values) and the most diversified (in Simpson diversity values) fish communities.

Thirdly, downstream sectors, marking the beginning of the mesotidal portion of the fluvial estuary, are home to distinct fish communities compared to the upstream part of the river (seen also by Leclerc et DesGranges 2005). 6-BB and 7-GSN are composed of fluvial and estuarine species (e.g. *Microgadus tomcod, Acipenser oxyrinchus, Morone saxatilis*) due to their position along the longitudinal gradient. While only a few species were captured in 7-GSN, the local diversity is nevertheless important thanks to the average taxonomic difference existing between constituent species. Such observation is associated with (1) the smaller number of congeneric species found locally for species families (i.e. Centrarchidae, Cyprinidae) and (2) the simultaneous presence of species from the upper freshwater portion of the river together with estuarine / euryhaline species (e.g. *M. tomcod*) from the estuary bringing together distantly related species.

Longitudinal patterns from headwater toward the mouth were observed by several studies targeting small to medium-size rivers (e.g. Belliard *et al*. 1997; Araùjo *et al*. 2009; Wu *et al*. 2011). In large rivers, such as the Gange and the Mekong, the middle part of the river appears as the most diversified along the continuum when

considering the specific fish diversity (e.g. Simpson diversity, Das *et al*. 2013; Chea *et al*. 2016). This pattern is also observed in the St.Lawrence for Simpson diversity and the rarefaction index (Figure 1.2). The presence of phylogenetically-distant estuarine and marine species observed in the lower part of large rivers is a likely reason explaining the local increase in taxonomic diversity at the end of the river continuum (i.e. river mouth).

1.5.2 Spatial heterogeneities at different scales

Even if both man-made longitudinal discontinuities (e.g. upstream dams) and riverscape heterogeneities are contributing to the longitudinal gradient observed in the St. Lawrence fish communities, a more complex and patchy organisation appear when considering the fish community at different spatial scales. As for results observed in the upper Mississippi (Chick *et al*. 2005), our results suggest a hierarchical structure of the spatial organisation in the St. Lawrence fish community. Firstly, contrasted hydro-geomorphological units along the river, such as the presence of a fluvial lake, largely increase habitat heterogeneity and may be seen as discontinuities along the continuum supporting different communities (e.g. plankton communities; Hillbricht-Ilkowska 1999). Large fluvial lakes contain more shallow habitats with limnophilic and vegetation-dependant species than corridor units typified by deep habitats and high current velocity with more rheophilic species (Leclerc et DesGranges 2005).

Secondly, at sector scale (≈ 15 50 km), it appear that every sector identified according to their specific hydrological and morphometric characteristics hosted significantly distinct fish communities. Similar to the situation observed in the upper Paraná River (Agostinho *et al*. 2007; Ferrareze *et al*. 2014), our result confirms the importance of uniqueness in fluvial landscapes (Poole 2002) which largely determine the fish community structure in large rivers. The type of spatial heterogeneity observed in each sectors such as the numerous islands and channels of the 4-A-LSP, the extensive

floodplain of the 5-LSP, and the tidal movement in 7-GSN, appears as key elements structuring fish communities organisation of the St. Lawrence River.

Thirdly, when the heterogeneity of physical and biological conditions prevailing independently along either shore of a large temperate river are considered, such as in the St. Lawrence river, the global fish communities organisation revealed a much more complex pattern. To our knowledge, large rivers have been never studied at the shore scale. However, this finer scale allowed highlighting similarities between adjacent sectors and transversal discontinuities within sectors in the St. Lawrence River. The 4-A-LSP and the nearby Maskinongé bay (see Figure 1.1) identified as a productive habitats, seem to influence fish community structure of the upstream part of the 5-LSP, which contribute to fish community similarities along north shore (seine nets results, Figure 1.3). More surprisingly, the downstream part of the 5-LSP and the 6-BB sector have similar communities (using the seine nets data, Figure 1.3) suggesting an higher homogeneity between these two sectors that previously expected considering that they are different hydro-morphological units. Since the 4-A-LSP and the 5-LSP are both considered highly productive areas (e.g. Tall *et al*. 2008; Mingelbier *et al*. 2016), they have the potential to "export" surplus production downstream (e.g. plankton; Basu *et al*. 2000) in sectors where emigrant fishes will eventually contribute to homogenize local communities. Moreover, results revealed differences between fish communities along north and south shores in several sectors of the St. Lawrence River. The local heterogeneity of habitats along each shore (e.g. watershed land use, hydro-geomorphology, tributaries etc.), in some areas the large distance between opposing shores (e.g. ≥ 11 in 2-LSL and 5-LSP) and, for several species, the large (≥ 300 m) and deep (≥ 8.2 m) navigation channel that may prevent fish dispersal (Leclerc et DesGranges 2005; Leclerc *et al*. 2008) can account for the significant transversal differences observed in the St. Lawrence River. Even if the main channel can be a barrier for only some species (e.g. *Perca flavescens*, Leclerc *et al*. 2008) and not to the entire riverine specialists, the limited dispersal capacity of

only a few species may change the overall community structure and diversity. Furthermore, the dominant land use in watershed and the water masses flowing along the north (suburban landscape, brown waters of the Ottawa River) and south (agricultural and industrial landscapes, green waters of the upper St. Lawrence River) shores of the 2-LSL are likely contributor to the perceived differences between northern and southern sector of the lake. Downstream in the 4-A-LSP, the southern sector is close to the navigation channel whereas the northern sector is made out of multiple islands and numerous small channels (Figure 1.1). The Yamaska and Saint-François tributaries drains polluted waters into the southern region of 5-LSP (MDDEP 1998; Hudon et Carignan 2008) which had deeply impacted the vegetation (an important loss of the underwater vegetation). As the tributaries' waters did not cross the central navigation channel, they had not impacted the northern part of 5-LSP. Finally, the north shore of 6-BB is largely artificialized while the south shore is composed of large vegetated shoals similar to what was the 5-LSP until recently.

1.5.3 Implications for management

1.5.3.1 Unexpected diversity pattern

While considering the general spatial pattern of diversity, we identified two sectors exhibiting levels either much higher (i.e. 6-BB) or lower (i.e. 5-LSP) than expected (Mingelbier *et al*. 2008b). Rarely considered as a hotspot for diversity, the little studied downstream Bécancour-Batiscan (6-BB) sector exhibits high values of rarefaction, Simpson diversity and taxonomic distinctness for both fish communities captured by seine and gillnet (Figure 1.2). The 6-BB is located downstream of the Lake Saint-Pierre (5-LSP), with large vegetated shoals along the southern shore. These results emphasize the importance of better describing this sector in the eventuality of formulating plans to protect its biodiversity. In contrast, elevated values for fish diversity indices were expected for the 5-LSP thanks to the sheer size of the area and the diversity of fish habitats it contains. The 5-LSP is an extensive

marshland due to its shallow topography (mean depth 2.7 m, maximum depth 13.7 m; Carignan et Lorrain 2000) with ubiquitous macrophyte beds and large floodplains generated during spring freshets (up to 54 500 ha; Richard *et al*. 2011). However, the values of rarefaction, Simpson diversity and taxonomic distinctness of the community collected by seine were lower than expected if LSP should be a hotspot of diversity (i.e. the LSP was not the richest and more diversified sector along the St. Lawrence River). Cumulative human pressures in the 5-LSP may partly explain this pattern. For example, the advent of intensive agricultural practices (e.g. corn and soy) on the 5-LSP floodplains has been identified as a primary cause for the collapse of the once locally super-abundant yellow perch (de la Chenelière *et al*. 2014).

1.5.3.2 Specific and Taxonomic diversity patterns

Specific and taxonomic diversity indices revealed different hotspots along the St. Lawrence River (e.g. 4-A-LSP and 7-GSN sectors). Since taxonomic diversity considers the evolutionary relationships within fish communities, it explicitly incorporates species differences rather than just the number of species that may be taxonomically-redundant. In the St. Lawrence, while the number of fish families observed in the 4-A-LSP is higher than in the 7-GSN sector, the elevated number of congeneric species in the 4-A-LSP (i.e. Cyprinidae, Centrarchidae and Percidae; appendix Table A.2) lowers the value of the taxonomic diversity. For this reason, a higher taxonomical fish diversity is observed in the 7-GSN sector. Recognizing the difficulties associated to decision-making when prioritizing which areas should be protected in the face of limited financial resources, protecting the highest number of species possible without further consideration (e.g. ecological role, taxonomical redundancies, overall rarity, etc.) is not necessarily the most rewarding action; for the St. Lawrence River fishes community, the taxonomic distinctness appears as a measure worth further considerations (Vellend *et al*. 2011). Conversely, this index may be misleading as a seemingly “diversified” community may be the result of the combination of a few taxonomically-divergent species. Theses perspectives underline

the importance of considering simultaneously different measures of biodiversity in the overall evaluation of sites (e.g. richness species and taxonomic distinctness, Heino *et al*. 2005).

1.5.3.3 Management Units

Management units have to be based on the structure of fish communities taking into account ecological gradients, discontinuities and heterogeneities. Even if hydro-morphological characteristics are useful to delineate functional management units in the St. Lawrence River (i.e. sector units; Mingelbier *et al*. 2016), other elements or processes such as human disturbances and fish dispersal can influence the fish community organisation. The differences between shores as well as the continuity observed between several sectors (i.e. 4-A-LSP/5-LSP and 5-LSP/6-BB) could be useful to define new fish management units reflecting the observed heterogeneity of fish communities. Such differences were in fact observed in the genetic pattern of yellow perch (*Perca flavescens*) populations in the St. Lawrence River. Genetic discontinuities between the north and south shores of the 2-LSL were associated to the sedentarity nature of these two populations (Leclerc *et al*. 2008). Moreover, two sympatric populations of rainbow smelt (*Osmerus mordax*) found in the St. Lawrence Estuary were found to be spatially segregated along the north and south shores (Lecomte et Dodson 2004; Dodson *et al*. 2015). Then, spatial processes observed at a broader scale (e.g. longitudinal dynamics) improve our understanding of how fish community is organised at the scale of the sector.

1.5.3.4 The usefulness of large and standardised sampling program

Only the system-wide, multiannual and standardised surveys have allowed the detection of patterns within the fish community organisation along the St. Lawrence River. The RSI has captured to date almost a third of a million fishes, including rare species such as *Moxostoma valenciennesi*, *Ammocrypta pellucida* and *Noturus flavus* (appendix Table A.2). However, the selectivity of gears used, the sampling period

(e.g. some migratory species were not in the area at the moment of sampling) and the fact that some habitats were not sampled by the RSI (e.g. rapids, navigational channel) limits our ability to capture all species exploiting the St. Lawrence River (i.e. 97 fish species) and accurately quantify densities for several species (e.g. *Anguilla rostrata*, lampreys, alosines, salmons, carps). For example, whereas millions of *Anguilla rostrata* have migrated in the St. Lawrence River (Guillemette *et al*. 2014), only two were found in our samples. While this dataset has already revealed key observations since 1995 (e.g. stocks collapse and spread of invasive species; La Violette *et al*. 2003; Mingelbier *et al*. 2016) we consider that the RSI reflects the abundance of the vast majority of species present in the system and allows depicting how communities are structured along the St. Lawrence River.

1.6 Acknowledgments

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CHAPITRE II

THE MANY FACETS OF CONNECTIVITY: MODELLING THE EFFECTIVE SPAWNING AND NURSERY HABITATS WITHIN A LARGE SPATIO-TEMPORALLY VARIABLE RIVER LANDSCAPE (ST. LAWRENCE RIVER, CANADA)

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2.1 Abstract

Spawning and nursery habitats are often spatially disjunct as a consequence of distinct life history stage, specific habitat requirements and through spatio-temporal habitat changes. Nevertheless, free-swimming larvae located on spawning habitats must reach productive nursery areas to maximize recruitment. To quantify how habitat connectivity interacts with hydrological variability in altering the distribution of effective spawning habitat, we used northern pike (*Esox lucius*) as a model species. Habitat models coupled to a least-cost approach were developed to quantify connectivity between spawning and nursery areas in two contrasted regions of the St.

Lawrence River (Canada): a riverine corridor and a large fluvial lake. Our simulations demonstrate that depending on hydrological conditions, between 3 to 51% of spawning habitat used by adults in the corridor, and 22 to 90% in the lake, allowed larval survival up to the 5th week of development. Although rapid dewatering of spawning habitat is responsible for most spawning potential in the lake, increasing water currents were responsible for dispersing larvae away from suitable habitats in the corridor. On the other hand, stable hydrological conditions led to spatial overlapping of spawning and nursery habitats favouring larval survival and growth. Alternatively, downstream larval dispersal by low water currents allowed larvae to reach spatially disjunct nursery habitat, especially in the lake. This indicates that despite the vast areas of potentially suitable habitats provided by the large vegetated floodplains of fluvial lakes, the effective spawning habitats favouring early-life recruitment are much more heterogeneous and extremely variable both spatially and temporally.

Keywords: northern pike, least-cost modelling, riverscape, flow variability, passive transport, larvae mobility.

2.2 Introduction

Most marine and freshwater fishes exhibit complex life cycles during which spatially disjunct habitats are sequentially exploited (Sinclair 1988; Schlosser 1995). In this perspective, constraints to habitat connectivity may impair life cycle completion, a threat greatly enhanced during early-life history stages of most fishes (Dahlberg 1979). Although numerous studies in marine systems have highlighted the pivotal role played by habitat connectivity for larval fish survival and recruitment (Sinclair 1988; Secor 2002; Houde 2008), its role in freshwater environments is far less acknowledged (Falke *et al*. 2013; Ludsin *et al*. 2014; Goto *et al*. 2015).

The energetic costs and mortality risks associated with movement among different landscape features was first considered by Baudry et Merriam (1988) in terrestrial landscape ecology. In the context of riverine landscape ecology (Wiens 2002), when considering together physical connectivity of landscape features, spatio-temporal variability of environmental conditions, individual dispersal capacity and early life history habitat requirements, presumably good spawning habitats may become mortality traps if eggs spawned locally are unable to hatch and larvae are unable to reach nursery habitats (e.g. Jeffres et Moyle 2012; Hufnagl *et al*. 2013; Sheaves *et al*. 2014). Thus, we define *effective spawning habitats* as those habitats permitting the survival of eggs and larvae, and their access to nursery areas from which they may recruit to the adult population.

In aquatic environments, spatio-temporal variability of hydrological conditions (e.g. flood pulse and water flow direction) exerts a strong influence on habitat connectivity (Junk *et al*. 1989; Wiens 2002). Seasonal variations in water discharge may temporarily connect productive areas such as estuarine pools and riverine floodplains to main water masses (Gorski *et al*. 2011; Davis *et al*. 2012). Consequently, rapid decrease of water discharge at the beginning of the life cycle may suddenly dewater or isolate spawning habitats from nursery area, which can result in massive egg and larvae mortality (Dumont et Fortin 1977; Fortin *et al*. 1982; Žiliukienė et Žiliukas 2012). Moreover, interannual fluctuations in hydrological conditions are likely to change the spatial distribution of spawning habitats and nursery areas, which directly influences yearly fish recruitment variability (e.g. Hufnagl *et al*. 2013; Goto *et al*. 2015).

To exploit spatially-disjunct habitats, newly hatched larvae may employ (1) active behavioural mechanisms such as selective tidal-stream transport (e.g. Robins *et al*. 2013) and vertical migration (e.g. Ospina-Alvarez *et al*. 2012), or (2) passive mechanisms that exploit climatic forces such as winds (e.g. Soto-Mendoza *et al*.

2012) and water currents (e.g. Hare *et al*. 2002). As larval fish exhibit limited swimming capacities, passive processes are believed to predominate over behavioural mechanisms for long-distance larval dispersal (e.g. many kilometers, Dettmers *et al*. 2005; Dickey-Collas *et al*. 2009). As such, water current speeds were described as a key factor explaining larval dispersal and survival of several fish species (e.g. Heggenes et Traaen 1988; Hare *et al*. 2002; Schiemer *et al*. 2003).

Habitat connectivity can be studied in aquatic environment using individual-based (e.g. Ospina-Alvarez *et al*. 2012; Rochette *et al*. 2012; Soto-Mendoza *et al*. 2012) or habitat-based models (e.g. Le Pichon *et al*. 2006b; Isaak *et al*. 2007; Falke *et al*. 2013). A least-cost approach, coupled to habitat models, have proven successful in considering the interaction of landscape features and the species' dispersal capacity in estimating the degree of habitat connectivity. In this approach, every landscape feature is assigned a 'resistance' value according to its facilitating/impeding effects on animal movements (Adriaensen *et al*. 2003). Notably, the least-cost path is not necessarily the shortest distance between two habitats but rather the path involving the smallest energetic costs. Least-cost approaches were recently used to quantify how aquatic landscape features, such as current speed and direction, substrate types, availability of shelters, facilitate or impede fish movements in freshwater landscapes (i.e. the riverscape, Hanke *et al*. 2013) or in marine landscapes (i.e. the seascape, Caldwell et Gergel 2013).

In the present study, we used habitat models coupled with a least-cost approach to quantify how habitat connectivity interacts with hydrological variability in modulating the extent and distribution of effective spawning habitats in a large river system. We used the northern pike (*Esox lucius*), a typical early-spring floodplain broadcast spawner, as a model species. The species' early life-history requirements are well defined (e.g. Fortin *et al*. 1982; Inskip 1982; Vallières et Fortin 1988) and northern pike recruitment is known to be influenced by hydrological conditions

(Johnson 1957; Dumont et Fortin 1977). Finally, recent declines in northern pike abundance observed in several large river systems (Boët *et al*. 1999; Raat 2001), including the St. Lawrence River (Smith *et al*. 2007), stresses the need to assess large-scale environmental causes behind wide-spread recruitment failure.

Specifically, the distribution of potential northern pike spawning and nursery habitats in the St. Lawrence River was modelled for the period covering 1965-2013 to (1) quantify and compare the potential to the effective spawning habitats (i.e. connected to a nursery), (2) estimate the role of water discharge variations, current speeds, and larval dispersal on the connectivity between spawning and nursery habitats and (3) assess the spatio-temporal variability of effective spawning habitats during contrasted hydrological conditions representative of the system's annual variability. The analyses were performed on two ecologically distinct regions of the St. Lawrence River: a vast fluvial lake (the Lake Saint-Pierre) and a narrow and fast flowing riverine corridor (St. Lawrence River between Montréal and Sorel). To fulfil these objectives, we used 2-D hydrodynamic and biological models developed by Environment Canada for the St. Lawrence River (2,260,821 20mx20m cells) covering the 1965-2013 period (Morin *et al*. 2005).

2.3 Methods

2.3.1 Study area

The St. Lawrence River (thereafter SLR: Figure 2.1) is one of the world's largest rivers with a watershed area (excluding the Great Lakes watershed) of 1,344,200 km^2 and a mean annual discharge of 10,270 $m^3.s^{-1}$ at Sorel (Morin et Bouchard 2000). This river flows from the Great Lakes to the Atlantic Ocean (Figure 2.1). Along the SLR, fluvial lakes alternate with narrow sections and archipelagos whose physiographic and hydrologic characteristics vary in time and space. Even if the SLR discharge is partially regulated upstream of Montréal since 1912 (Carpentier 2003), the interannual variability in spring water discharge is nevertheless ranging from

6,500 to 17,500 m^3/s at Sorel (1965-2013) which maintains an extensive floodplain between Montréal and Trois-Rivières (Figure 2.2; Morin *et al*. 2005). The spatio-temporal heterogeneity of habitats along the SLR supports a diverse fish community totaling 97 freshwater and anadromous species (Foubert *et al*. submitted, see chapter I in the present thesis).

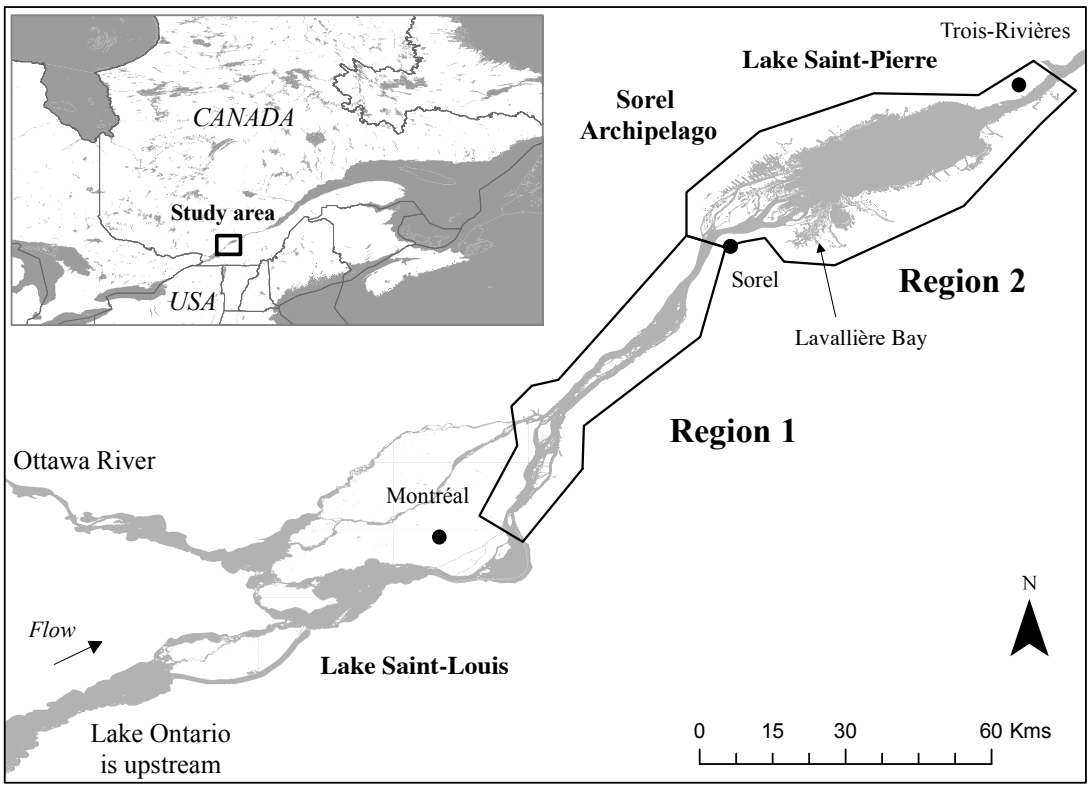

Figure 2.1 The fluvial portion of the St. Lawrence River (SLR, Québec, Canada) and the two hydrological regions studied: Region 1 corresponded to the narrow corridor between Montréal-Sorel and Region 2 to the large fluvial Lake Saint-Pierre and its archipelago.

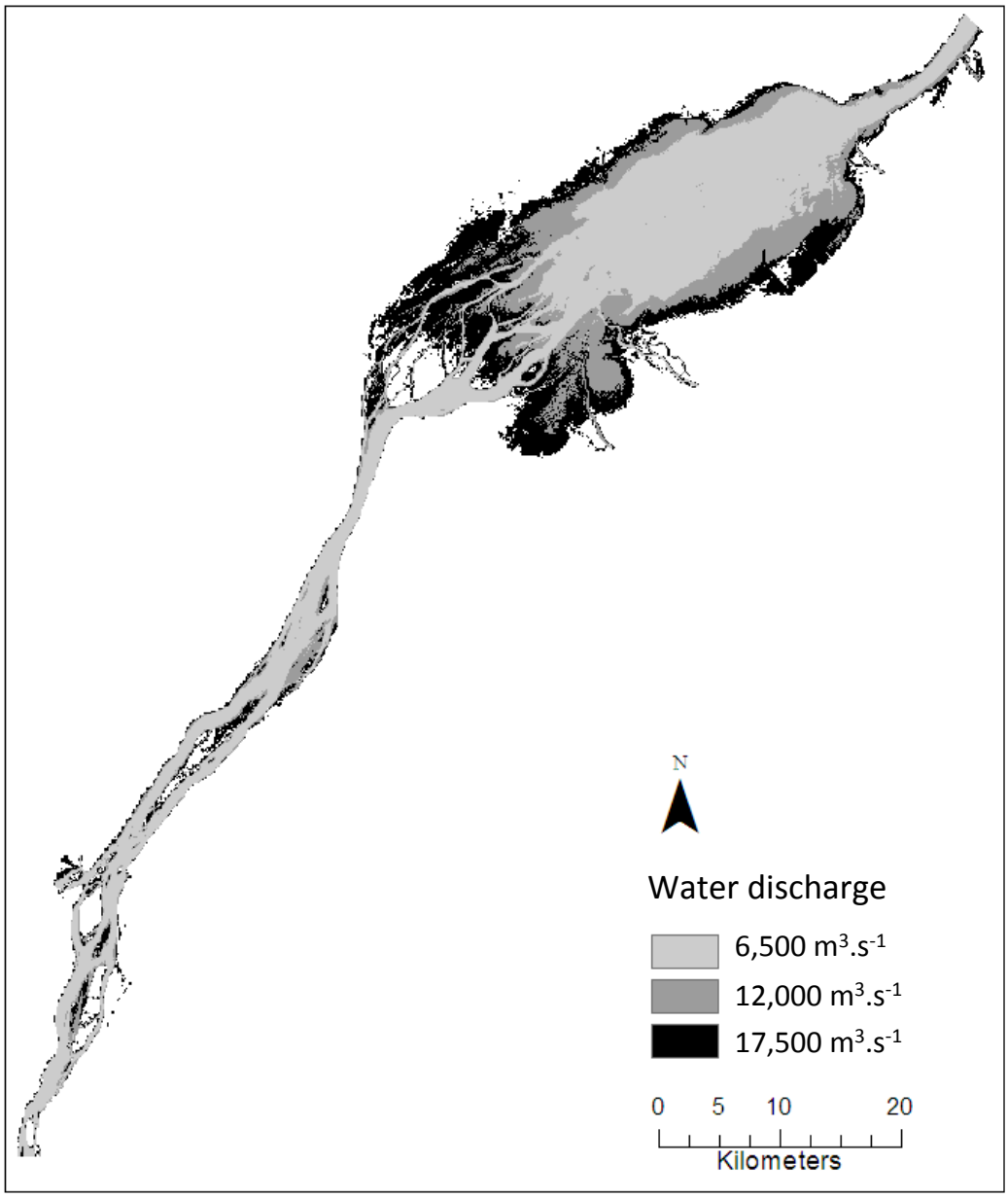

Figure 2.2 Extension of the floodplain in the study area for water discharges of 6,500 $m^3.s^{-1}$ (42,610 ha), 12,000 $m^3.s^{-1}$ (61,764 ha), and 17,500 $m^3.s^{-1}$ (80,446 ha) as measured at Sorel gauging station (St. Lawrence River, Québec, Canada).

In the present study we compared two distinct ecosystems of the SLR between Montréal Harbor and Trois-Rivières (Figure 2.1). The first region (hereafter referred to as the Montréal-Sorel corridor) consists of a narrow corridor located between Montréal and Sorel (46 km long, 3 km wide) characterized by elevated current speed and few islands. The second region (hereafter referred to as the Lake Saint-Pierre) includes the large fluvial Lake Saint-Pierre (25.6 km long, 12.8 km wide) and its associated archipelago (22.4 km long, 10.5 km wide, including 103 islands located immediately upstream of the lake). This region was listed in 2000 as a UNESCO Word Heritage Biosphere to protect this unique ecosystem. The gentle lateral bottom slope (depth <3 m) of the Lake Saint-Pierre combined with low current speeds (<0.5 $m.s^{-1}$) and extensive macrophyte beds (Centre-Saint-Laurent 1996) makes this lake resemble a gigantic marshland.

2.3.2 Habitat modelling from 1965 to 2013

Two-dimensional hydrological and biological models developed by Environment Canada (Morin et Bouchard 2000; Turgeon *et al*. 2004; Morin *et al*. 2005) were used to generate Habitat Suitability Indices (HSI) for spawning and nursery habitats in the SLR. These spatially-explicit models are calibrated using field observations. The models are able to generate water depths, current speeds, wetland types, and potential water temperatures on a weekly resolution for 2,260,821 cells representing the entire SLR between Montréal and Trois-Rivières (regular square grid, each cell covering 20 m x 20 m). The models simulate the extent of flooding and the succession of wetlands for the period covering 1965 to 2013 by not considering human land-use activities such as agriculture and transport infrastructures. Such "unaltered" landscapes were modelled to assess the intrinsic natural variability of the river and its impact on habitat connectivity.

We used an Habitat Suitability Index (HSI) for northern pike spawning habitat based on three variables: (1) current speed ≤10 $cm.s^{-1}$, (2) wetland types are deep marsh,

shallow marsh, shrub marsh, and meadow and (3) water temperature ≥7°C (see details in Mingelbier *et al*. 2008a). These variables were considered as the major drivers for spawning habitat selection among esocids (Johnson 1957; Fortin *et al*. 1982; Inskip 1982; Vallières et Fortin 1988; Casselman et Lewis 1996).

HSI for nurseries were calculated considering early larval pike requirements at the beginning of their free-swimming stage when they enter their nurseries; in the SLR this period is estimated to occur five weeks ($Week_5$) after the maximum spawning time ($Week_0$) (Fortin *et al*. 1982; Massé *et al*. 1988; Vallières et Fortin 1988). As hydrological and biological models used were based on a temporal scale (weekly values), we converted the early-life history development to weeks instead of °C*days. Larval pike habitat requirements were defined using both literature (Vriese *et al*. 1994; Casselman et Lewis 1996; Skov et Koed 2004; Cucherousset *et al*. 2009; Timm et Pierce 2015) and field observations in the upper SLR during spring 2014 (Foubert 2014, internship report). Larval requirements considered for calculating $HSI_{nursery}$, include: (1) water depth ranging from 39.0 cm to 100.0 cm, (2) current speed ≤10 $cm.s^{-1}$ and (3) presence of previous' year emergent vegetation that protect larvae from waves. Early in spring, northern pike spawn over moribund and perennial emergent plants that grew the previous summer (Timm et Pierce 2015). Submerged plants were not considered in our simulations as most material break down during fall, very little of theses plant structures persist after winter (Morin *et al*. 2005).

2.3.3 Temporal analysis

The total surface area of $HSI_{spawning}$ (= potential spawning habitats) and $HSI_{nursery}$ (= potential nursery areas) were quantified for the period covering 1965 to 2013 in both regions using ArcGIS 10.1 and Modelbuilder, an automated add-on toolkit from ArcGIS package. Spearman's Rank Correlation Coefficient was used to evaluate (1) the annual relationship between the total potential spawning and nursery areas, (2) the relationship between the total area of potential spawning habitat and water discharge

at the moment of spawning ($Week_0$) and (3) the relationship between the total potential area of nursery habitat and the water discharge at the moment larvae became free-swimming ($Week_5$).

2.3.4 Spatial analysis

The software *Anaqualand 2.0* (Le Pichon *et al*. 2006a) was used to quantify the spatial structure of habitats, their fragmentation and habitat connectivity (e.g. Le Pichon *et al*. 2009; Acolas *et al*. 2012; Carnie *et al*. 2016). *Anaqualand 2.0* estimates least-cost paths (i.e. minimal cumulative resistance, Adriaensen *et al*. 2003) between habitat patches for either upstream or downstream movement or for both directions. Least-cost paths integrating impediments (e.g. physical barriers) and/or facilitations (e.g. passive transport) to movement are compiled in 'Functional Distance' maps. Finally, *Anaqualand 2.0* converts 'Functional Distance' maps in 'Accessibility' maps considering fish mobility (see Figure 2.3 and appendix Figure B.1 for more details).

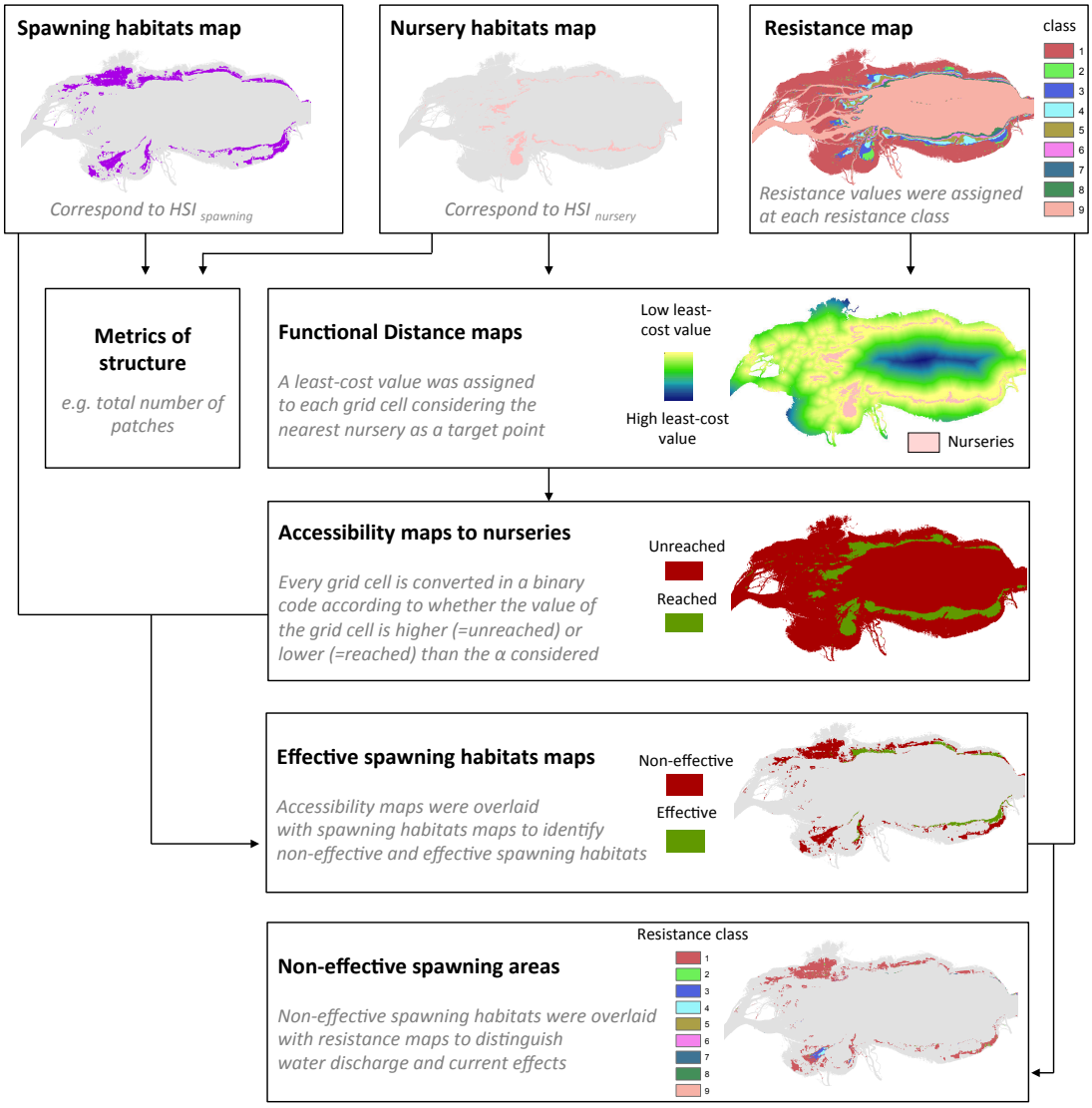

Figure 2.3 Flowchart explaining the spatial analysis used to model northern pike effective spawning habitats in both studied regions of the St. Lawrence River. The decreasing water discharge between the spawning time ($Week_0$) and the free-swimming stage ($Week_5$) observed in spring 1998 in the Lake Saint-Pierre was used to illustrate each steps performed with *Anaqualand 2.0* and *Arcgis 10.1*.

2.3.4.1 Input data in *Anaqualand 2.0*: habitat and resistance maps

Anaqualand 2.0 inputs were habitat maps (here $HSI_{spawning}$ and $HSI_{nurseries}$ described above) and resistance maps generated by *ArcGIS 10.1* in raster files format (ascii type; Figure 2.3). Resistance maps reflect the impacts of water discharge and current speeds on egg survival and larval dispersal. Nine resistance classes were calculated by combining two variables generated by Environment Canada's SLR models (see description above): dewatering surfaces between $Week_0$ and $Week_5$ (one class), and current speeds during $Week_5$ (eight classes ranging from 0 to 14 $cm.s^{-1}$ [2 $cm.s^{-1}$ increments], appendix Table B.1).

2.3.4.2 Resistance values

Two different sets of resistance values were performed. In the first set, resistance values were assigned to every class defined in the resistance map: (1) a resistance value of 1 involves unaided upstream and downstream movements (i.e. only larval swimming capacity is considered) and was assigned for current speeds ranging between 0 and 2 $cm.s^{-1}$, (2) resistance values <1 involve facilitated downstream dispersal (larval drift aided by currents) and was assigned to current speeds ranging from 2 to 10 $cm.s^{-1}$; (3) a maximum resistance value of 10,000 (preventing any survival or successful dispersal) was assigned to areas dewatered between $Week_0$ and $Week_5$ and areas where current speeds >10 $cm.s^{-1}$ (appendix Table B.1). In the second set, resistance values did not integrate current facilitations: a resistance of 1 was fixed for all grid cells where current speeds ranged between 0 and 10 $cm.s^{-1}$. It allowed us to quantify the distance travelled by larvae not aided by downstream currents.

Although the value of 10 $cm.s^{-1}$ is considered as the maximum current speed larval pike are able to sustain without suffering injuries or mortality (Peake 2004), we conducted sensitivity analyses considering resistance threshold values of 12 $cm.s^{-1}$ and 14 $cm.s^{-1}$ to investigate if the threshold of 10 $cm.s^{-1}$ is a limiting factor (appendix Table B.1). In addition, sensitivity analyses were conducted on the gain in surface

area of effective spawning habitats resulting from larvae being able to swim upstream against current speeds ranging between 0 and 2 $cm.s^{-1}$.

2.3.4.3 Metrics of structure and fragmentation

The structure of potential spawning and nurseries areas were described using standard riverscape metrics such as the total number of patches, the total surface of patches and the mean individual patch surface (Carnie *et al*. 2016). In addition, habitat fragmentation was described using the mean proximity index, a distance-weighted area-based metric developed by Gustafson et Parker (1994) and adapted for the aquatic environment by Le Pichon *et al*. (2006b). This index quantifies the degree of habitat isolation in relation to its neighbors within a radius of specified instream distance (set to 6,000 m). The mean proximity is a dimensionless index and increases as patches are less isolated and less fragmented (Gustafson et Parker 1994). Its ability to detect the effects of the natural hydrological variability on habitat fragmentation was demonstrated by Le Pichon *et al*. (2009).

2.3.4.4 Functional distance maps

Functional distance maps were generated by combining the information provided by nursery habitats and resistance maps (Figure 2.3, appendix Figure B.1). The result is a 20 m x 20 m grid in which a specific least-cost value (i.e. minimal cumulative resistance, Adriaensen *et al*. 2003) is associated to each grid cell considering the nearest nurseries as a target point. For example, a grid cell close to a nursery, where resistance values do not restrain the connectivity (habitats shown in yellow on Figure 2.3), will be associated to a low least-cost value. This allows evaluating the potential for a larvae hatched from a specific spawning habitat to reach neighboring nurseries (the focus is on the spawning habitat).

2.3.4.5 Mobility coefficient (α)

The mobility coefficient (α) used in the present study is a metric reflecting the larval dispersal capacity across the landscape. The α value was derived from stage-specific larval swimming capacities at the beginning of their free-swimming stage ($Week_5$) and potential passive transport provided by local currents during this week ($Week_5$, appendix Table B.1). The maximal value was set to α = 6,000 m which corresponds approximately to the maximal distance travelled at 1 $cm.s^{-1}$ by a particle travelling the water column in a straight line over a one week period. Since larvae can modulate their passive dispersal through behavior (e.g. selecting slower bottom currents, migrating in the water column, seeking refuge in vegetation or exploiting physical features reducing advection), we conducted sensitivity analyses using α values set at 3,000, 1,500, 600, 300, 150 and 60 m.

As α is a distance integrating the least-cost value, it does not correspond directly to a physical instream distance when considering current facilitations (e.g. in the first set of resistance values). The modified distance is equivalent to 'functional meters' (e.g. $\alpha = 600 = 600\ m_{functional}$). In contrast, as the second set of resistance values did not integrate downstream current facilitations, α becomes directly equivalent to the maximal instream distance the larvae were able to travel (e.g. α = 600 = 600 m).

2.3.4.6 Accessibility maps

Functional distance maps were converted to accessibility maps using a threshold function available in *Anaqualand 2.0* (Roy et Le Pichon 2017). In this procedure, grid cells are converted to a binary code (unreached =0; reached =1) according to whether the functional map cell possesses a higher (=1) or lower (=0) value than the mobility coefficient α considered (Figure 2.3).

2.3.4.7 Effective spawning habitats

Accessibility maps were overlaid on potential spawning habitats ($HSI_{spawning}$) using *ArcGIS 10.1* to identify effective spawning habitats for each scenario tested (Figure 2.3). When a spawning habitat was located over an accessibility cell value =1 (nursery reached), it was considered as effective (i.e. connected to a nursery area). In contrast, when a spawning habitat was located over accessibility cell value =0 (nursery unreached), it was considered as non-effective (i.e. not connected to a nursery area). Thus, effective and non-effective spawning habitats were mapped and quantified (ha) for all α considered: 6,000, 3,000, 1,500, 600, 300, 150 and 60. In addition, the effect of mobility coefficients (α) and passive transport provided by currents on the total surface of effective spawning habitats (ha) were presented graphically. Finally, sensitivity analyses illustrate the effect of resistance threshold values (i.e. 12 and 14 $cm.s^{-1}$) on total surface of effective spawning habitats (ha: appendix Figure B.3).

2.3.4.8 Non-effective spawning habitats

Non-effective spawning habitats (i.e. lost to recruitment) were overlaid on the resistance map in *ArcGIS 10.1* (Figure 2.3) to distinguish (1) spawning habitats lost to dewatering occurring between $Week_0$ and $Week_5$ (class 1 of the resistance map; appendix Table B.1) from (2) spawning habitats lost because of fast current speeds (class 9) and (3) spawning habitats isolated by physical barriers preventing larvae reaching nurseries (class 2 to 8; Table 2. 2).

2.3.4.9 Contrasted hydrological conditions selected

Three flooding profiles during pike's springtime spawning period are recognized in the SLR: (1) the "typical" hump shape pattern where spawning occurs at the maximum water height followed by declining values, (2) profiles where water discharges continue to increase after spawning and (3) profiles when water level remained stable over the first few weeks after spawning. Historical analysis from the

years 1965 to 2013 revealed that frequencies of the three profiles are 53%, 14% and 33% respectively (Figure 2.4).

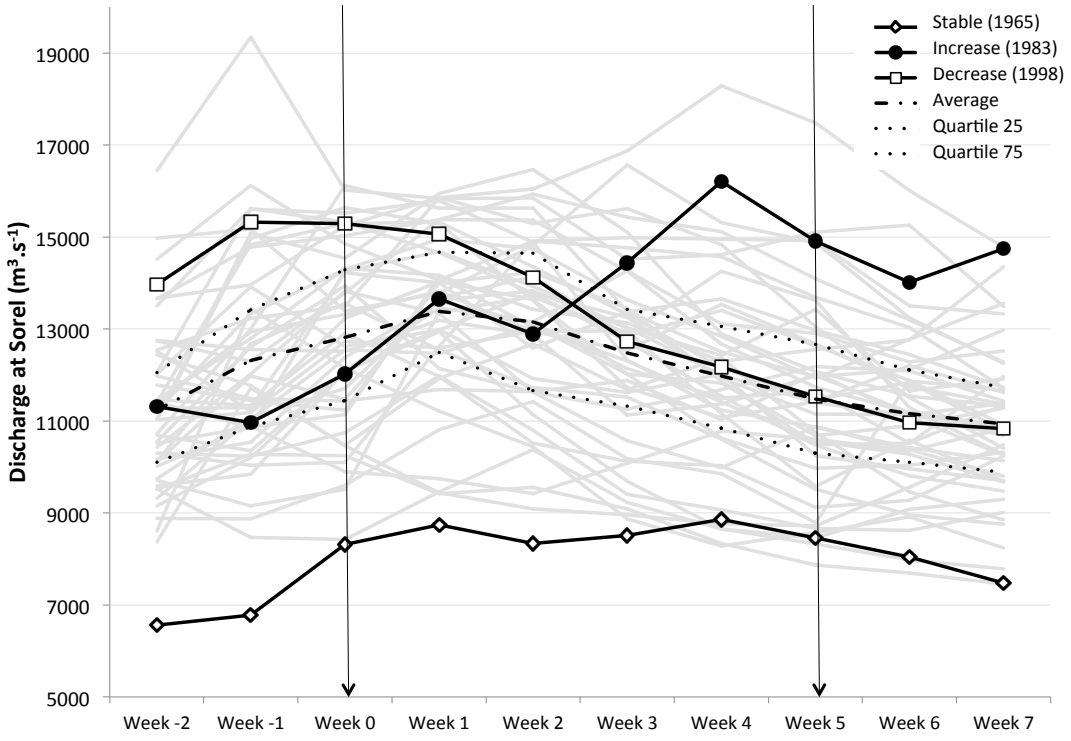

Figure 2.4 Weekly water discharge at Sorel gauge station (1965-2013) during the reproduction period of the northern pike (St. Lawrence River, Québec, Canada). $Week_0$ correspond to the maximum spawning time and $Week_5$ to the nursery period (i.e. free-swimming larvae). The spring flooding conditions (stable, increasing, decreasing) of the three selected years (1965, 1983, 1998) correspond to solid dark lines; the dotted lines correspond to the average profile (in bold) and quartiles (25%, 75%) calculated over the 49-year period.

Three years between 1965 and 2013 were selected to represent each of those profiles between the spawning time ($Week_0$) and the free-swimming period ($Week_5$): (1) the year 1998 corresponded to a high water discharge of 15,296 $m^3.s^{-1}$ at $Week_0$, decreasing to 11,532 $m^3.s^{-1}$ at $Week_5$, (2) 1983 corresponded to an "average" discharge of 12,021 $m^3.s^{-1}$ at $Week_0$ increasing toward $Week_5$ to reach 14,905 $m^3.s^{-1}$; and (3) 1965 corresponded to low but stable water discharges between $Week_0$ (8,315 $m^3.s^{-1}$) and $Week_5$ (8,455 $m^3.s^{-1}$). For comparison, over the period of 1965 to 2013, the average spring water discharge is 12,500 $m^3.s^{-1}$ at $Week_0$ and reduces to 11,000 $m^3.s^{-1}$ at $Week_5$ (Figure 2.4).

All analyses were performed for the three hydrological conditions selected and separately for the two regions studied (Montréal-Sorel corridor and the Lake Saint-Pierre).

2.4 Results

2.4.1 Temporal analysis

Both potential spawning and nursery habitat areas were highly variable annually over the period studied (1965-2013; Figure 2.5) and appear to depend mainly on water discharge and water recess. Historical records of the SLR water discharge between 1965 and 2013 ranged from 8,314 $m^3.s^{-1}$ to 16,121 $m^3.s^{-1}$ at $Week_0$ and from 7,866 $m^3.s^{-1}$ to 17,476 $m^3.s^{-1}$ at $Week_5$. The total potential surface area of the two habitats was correlated with the water discharge at $Week_0$ and at $Week_5$ in both regions considered (all four *p*-values <0.05, Spearman's rank correlation). However, although high water discharges generate larger potential spawning and nursery areas in the Lake Saint-Pierre (positive correlation), the same hydrological condition resulted in smaller surface areas of habitats available in the Montréal-Sorel corridor (negative correlation, see appendix Figure B.2). Over the entire period (1965-2013), using yearly values, the potential nursery habitat areas were not correlated with

potential spawning habitat areas in the Montréal-Sorel and Lake Saint-Pierre regions (two *p*-values >0.9, Spearman's rank correlation).

The greatest area of potential spawning habitat ranging between 2,001-7,261 ha and nursery habitat ranging between 1,151-5,822 ha was located in the Lake Saint-Pierre (Figure 2.5) where they occupying up to 14% of the total wetted area. The Montréal-Sorel corridor contained ten times less potential spawning (up to 668 ha) and nursery (up to 420) habitat areas than the Lake Saint-Pierre occupying only a maximum of 4% of the total wetted area.

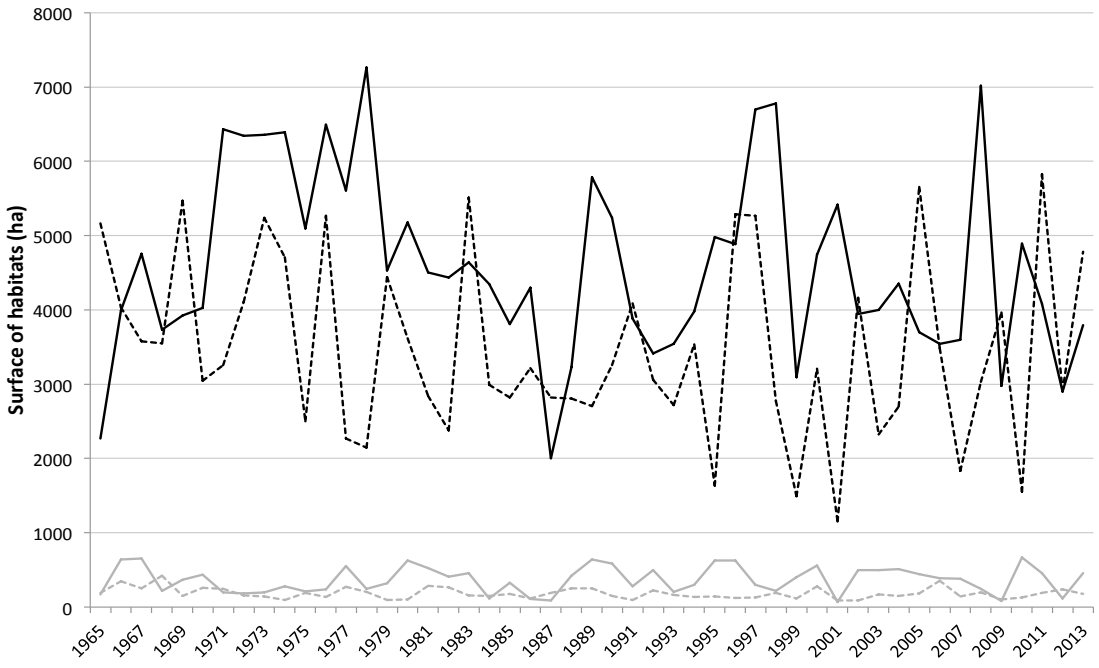

Figure 2.5 Northern pike habitats estimated for the period 1965-2013 in the Lake St-Pierre (black line) and the Montréal-Sorel corridor (grey line) of St. Lawrence River. The spawning habitat surface areas (solid line) were adapted from Mingelbier *et al*. (2008a) and the nursery habitat surface areas (dotted line) were estimated in the present study.

2.4.2 Spatial structure of spawning and nursery habitats

The spatial structure of potential spawning and nursery habitats changed in the two regions in relation to hydrological conditions (Table 2.1, Figure 2.6). In the Lake Saint-Pierre, a high water discharge resulted in the largest area of spawning (1998) and nursery habitats (1983), while a low water discharge led to the smallest area of spawning habitat (1965). A medium water discharge resulted in the smallest area of nursery habitat (1998). During the stable profile between $Week_0$ and $Week_5$ (1965), potential spawning habitat was more fragmented than in decreasing and increasing profiles whereas potential nursery habitat was less fragmented than in other profiles (see Proximity index values Table 2.1). During the increasing profile (1983), large area of potential spawning habitat was composed of larger patches than in the stable profile while potential nursery habitats were composed of the smallest individual patch areas despite their large total surface area. Given the increasing water discharge after spring spawning in 1983, potential nursery habitats were distributed higher on the upper edge of the floodplain (Figure 2.6). This situation was diametrically different of what was observed in stable and decreasing profiles. During the decreasing profile (1998), the largest potential spawning area and individual patch areas were observed whereas the decreasing water discharge at $Week_5$ resulted in the smallest potential nursery habitat area and small individual patch areas.

Contrasting with the situation observed in the Lake Saint-Pierre, an average water discharge, such as seen in 1983, created the largest potential spawning and nursery habitat areas in the Montréal-Sorel corridor, while low or high water discharges led to a smaller area of both vital habitats (Table 2.1). Indeed, the spatial structure of potential spawning habitat in the Montréal-Sorel corridor was comparable when water discharge is either high or low (1998 vs. 1965). While a high water discharge resulted in large potential habitat areas in the Lake Saint-Pierre, the increasing profile (1983) led to the smallest area of nursery habitat in the Montréal-Sorel corridor. However, a water discharge of average value, such as observed in 1983 at $Week_0$,

doubled the total area of potential spawning habitats in the corridor, which was less fragmented than in stable and decreasing profiles (see Table 2.1). Decreasing profile (1998) resulted in the largest potential area of nursery habitat in the corridor whereas the opposite situation was observed in the lake.

Finally, considering both regions of the SLR, our results revealed that potential nursery habitats were always more fragmented with a lower proximity index than potential spawning habitat independent of hydrological conditions (cf. Table 2.1).

Table 2.1 The total number of patches, the total surface of patches, the averaged surface of patches and the mean proximity index of spawning and nursery habitats for the three profiles (stable in 1965, increase in 1983, decrease in 1998) and the two contrasted regions studied in the St. Lawrence River (Québec, Canada). The mean proximity is a dimensionless index and increases as patches are less isolated and less fragmented. $Week_0$ correspond to the maximum spawning time and $Week_5$ to the beginning of free-swimming stage.

	Hydrological conditions		**Lake Saint-Pierre**					**Montréal-Sorel corridor**				
Years	Water discharge ($m^3.s^{-1}$)	Profile	Flooded surface (ha)	Habitat surface (ha)	Number of patch	Average surface of individual patch (ha)	Proximity Index	Flooded surface (ha)	Habitat surface (ha)	Number of patch	Average surface of individual patch (ha)	Proximity Index
1965												
Spawning habitats - $Week_0$	Low (8,315)	Stable	41,799	**2,527**	223	11	2.1	13,635	**202**	92	2	0.7
Nurseries - $Week_5$	Low (8,455)		42,981	**5,172**	329	15	1.5	13,943	**184**	121	1	0.6
1983												
Spawning habitats - $Week_0$	Medium (12,021)	Inscrease	49,800	**4,653**	207	22	2.7	14,976	**460**	135	3	1.2
Nurseries - $Week_5$	High (14,905)		61,305	**5,674**	656	8	1.5	15,752	**158**	84	2	0.6
1998												
Spawning habitats - $Week_0$	High (15,296)	Decrease	60,145	**6,791**	258	26	2.5	15,743	**219**	91	2	0.8
Nurseries - $Week_5$	Medium (11,532)		44,755	**2,782**	301	9	1.1	14,632	**202**	105	2	0.5

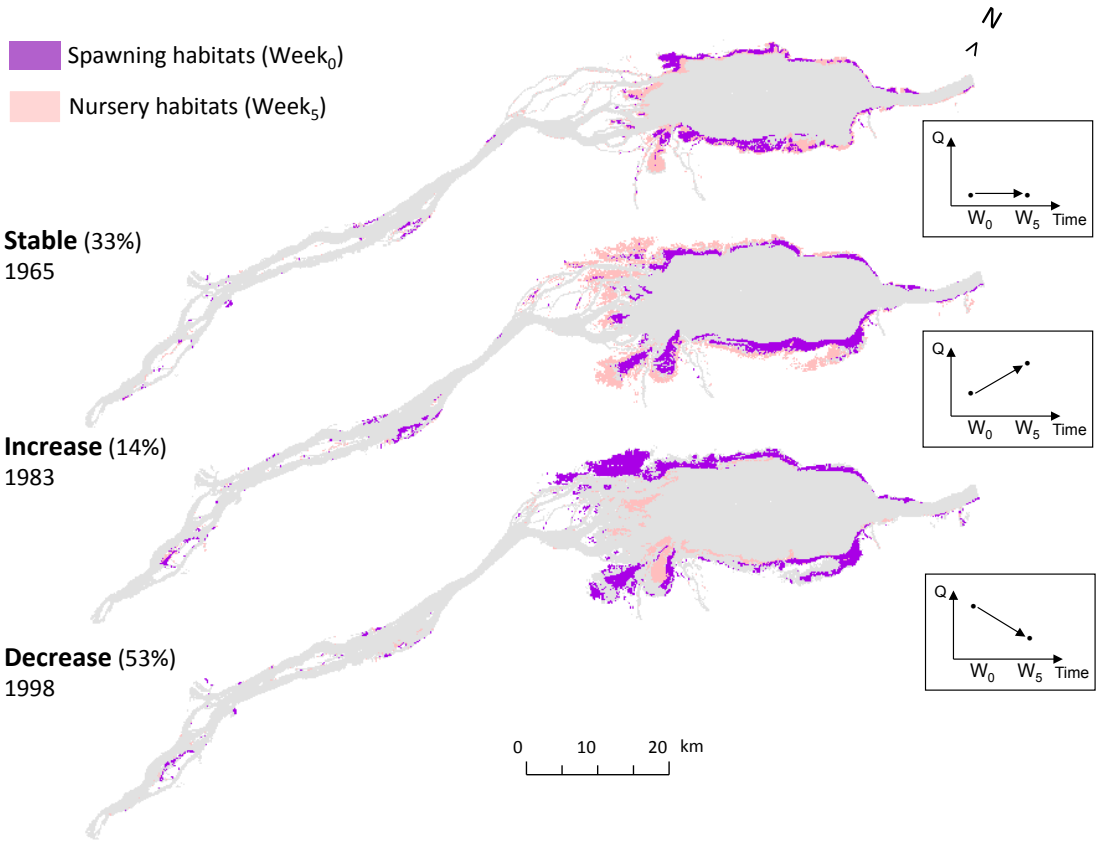

Figure 2.6 Localization of northern pike spawning and nursery habitats during stable (1965), increasing (1983) and decreasing (1998) profiles in St. Lawrence River (Québec, Canada) which occurred 33%, 14%, 53% respectively during the period 1965-2013. The water discharge (Q) between the maximum spawning time ($Week_0$) and the beginning of free-swimming stage ($Week_5$) are determinant for both the surface area and the spatial distribution of these habitats.

2.4.3 Effective and non-effective spawning habitats

Ten to 97% of potential spawning habitats were lost to recruitment as either eggs did not survived or larvae were unable to reach nurseries (see Table 2.2 and habitats indicated in red on Figure 2.7). Dewatering occurring in 1998 drained 70% of potential spawning habitat area of the Lake Saint-Pierre, while for the same period, 46% spawning habitat area were lost in the Montréal-Sorel corridor. Under any given hydrological condition, increasing water currents above the 10 $cm.s^{-1}$ thresholds after spawning resulted in a further loss of 1 to 17% of potential spawning area in the lake and 10 to 92% in the corridor. The greatest losses were observed during the increasing profile (1983). Moreover, even a slight increase of water discharge occurring between $Week_0$ and $Week_5$ in the corridor (e.g. 8,315 $m^3.s^{-1}$ to 8,455 $m^3.s^{-1}$ in 1965) triggered a loss of 50% of potential spawning habitat. In addition, dewatering and fast currents acted as physical barriers trapping larvae in natural pools (e.g. Lavallière bay in the Lake Saint-Pierre in 1998, see Figure 2.1) or impeding larvae to reach nurseries. Such phenomena explained a further loss of 1 to 6% of potential spawning habitat in the Lake Saint-Pierre and 5 to 6% in the Montréal-Sorel corridor (Table 2.2).

Table 2.2 Non-effective spawning habitats for the three profiles (stable in 1965, increase in 1983, decrease in 1998) in the two studied regions (St. Lawrence River, Canada). The surface area losses between potential and effective spawning habitats were explained by dewatering effects between the maximum spawning time ($Week_0$) and the beginning of free-swimming stage ($Week_5$), fast current speeds (>10 $cm.s^{-1}$) and the resulting physical barriers. The habitat surface area and their associated losses were expressed in hectares (ha).

Lake Saint-Pierre							
Year	Spring water discharge between $Week_0$ and $Week_5$	**Potential spawning habitats**	**Losses**				**Effective spawning habitats**
			Dewatering	Current speeds (>10cm.s^{-1})	Physical barriers	Total	
1965	Low and **stable**	**2,527**	0	222	22	244	**2,283**
1983	Medium and **increasing**	**4,653**	0	783	88	871	**3,782**
1998	High and **decreasing**	**6,791**	4,775	62	436	5,273	**1,518**
Montréal-Sorel corridor							
Year	Spring water discharge between $Week_0$ and $Week_5$	**Potential spawning habitats**	**Losses**				**Effective spawning habitats**
			Dewatering	Current speeds (>10cm.s^{-1})	Physical barriers	Total	
1965	Low and **stable**	**202**	0	102	12	114	**88**
1983	Medium and **increasing**	**460**	0	426	22	448	**12**
1998	High and **decreasing**	**219**	79	21	12	112	**107**

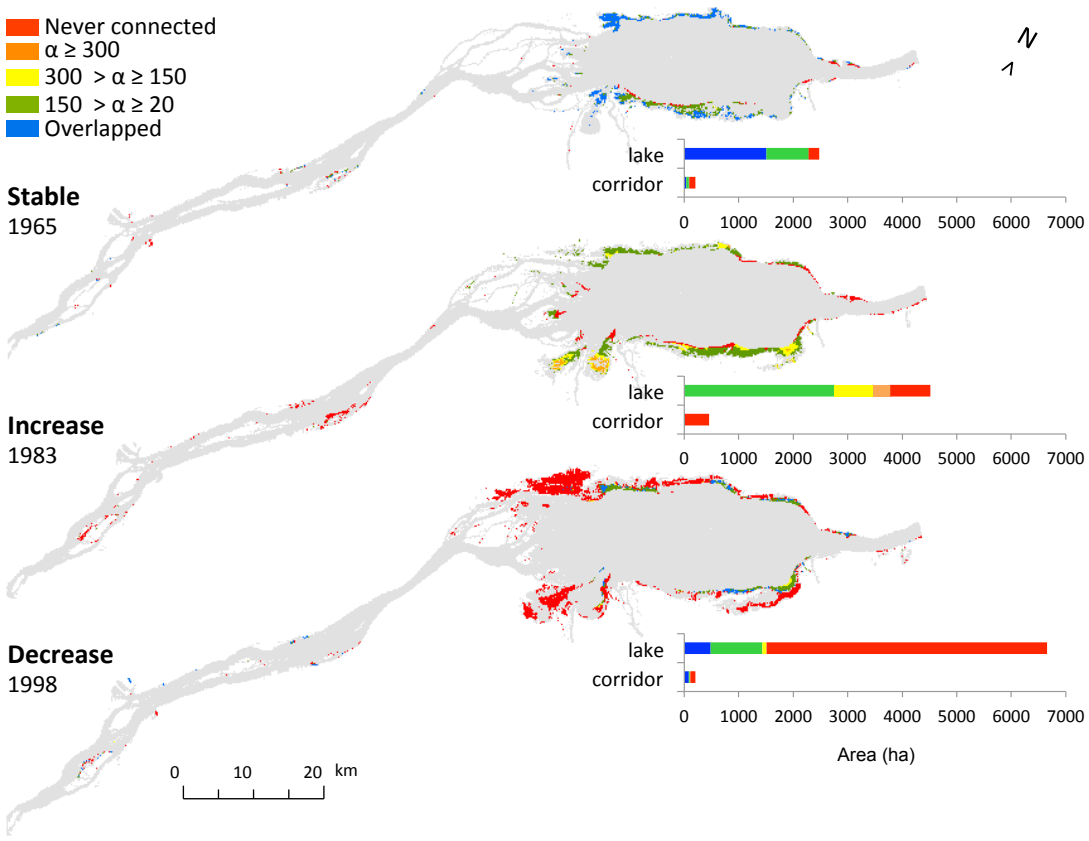

Figure 2.7 Non-effective and effective spawning habitats according to mobility coefficients (α between 60 m to 6000 m) for the three profiles (stable in 1965, increase in 1983, decrease in 1998) in the St. Lawrence River (Québec, Canada). Connectivity values correspond to five classes: (1) spawning habitats overlapping with nurseries (blue color), (2) spawning habitats connected when $\alpha \leq 150$ m $_{functional}$ (green color), (3) $150 < \alpha \leq 300$ m $_{functional}$ (yellow color), (4) $\alpha > 300$ m $_{functional}$ (orange color), and (3) spawning habitats which were never connected to any nursery (functional distance > α even with $\alpha = 6000$ m $_{functional}$; red color). As α is a distance integrating the minimal cumulative resistance (i.e. functional distance), the α unit is not equivalent to instream distance (i.e. international metric system).

The largest areas of effective spawning habitat observed in the Montréal-Sorel corridor occurred during the decreasing profile (1998) thanks to large spawning habitat areas generated at the moment of spawning ($Week_0$) and overlap that existed with nursery habitats. On the other hand, the largest areas of effective spawning habitat observed in the lake occurred during an increasing profile (1983) because "maximal mobility coefficient" (α = 6,000 $m_{functional}$) connected the large spawning surfaces to distant large nurseries areas. When potential spawning and nursery habitats where physically located on the same geographical position (i.e. physical overlap), this situation contribute in creating large areas of effective spawning habitat for both regions of the SLR (habitats shown in blue on Figure 2.7). In the Lake Saint-Pierre, the physical overlap of the two habitats reached 66% of all effective spawning habitat observed in stable profile (1965), 32% in decreasing profile (1998), while no overlap occurred in increasing profile (1983). In the Montréal-Sorel corridor, 38% of all effective spawning habitats overlapped in stable profile, 14% in increasing profile, and 75% in decreasing profile. As none or few potential spawning habitats overlapped in the increasing profile in both regions, the larvae mobility coefficients (α) that allowed reaching distant nursery habitats accounted for 100% of effective spawning habitat in the lake and 86% in the corridor (habitats shown in green, yellow and orange on Figure 2.7 depending on the α considered). Alternatively, the larvae mobility (α) is responsible for 34% of area considered as effective spawning habitat in stable profile and 68% in decreasing profile in the Lake Saint-Pierre, whereas an increase of 62% in stable profile and 25% in decreasing profile was observed in Montréal-Sorel corridor (Figure 2.8). However, the steadily increase of effective spawning habitat surfaces with increasing mobility coefficient (α) ceases at α = 300 $m_{functional}$ in stable profile, α = 1500 $m_{functional}$ in increasing profile and α =600 $m_{functional}$ in decreasing profile in the Lake Saint-Pierre. Furthermore, in the Montréal-Sorel corridor, the area of effective spawning habitat did not increase beyond 300 $m_{functional}$ in stable and decreasing profiles, and 150 $m_{functional}$ in increasing

profile (Figure 2.8). When considering physical instream distances (i.e. without current assistance between 0 and 10 cm.s^{-1}), the total area of effective spawning habitat stopped rising with a distance of 1500 m in stable profile and 3000 m in increasing and decreasing profiles in the Lake Saint-Pierre, whereas beyond 600 m, the area of effective potential spawning habitat did not increase in the Montréal-Sorel corridor (Figure 2.8).

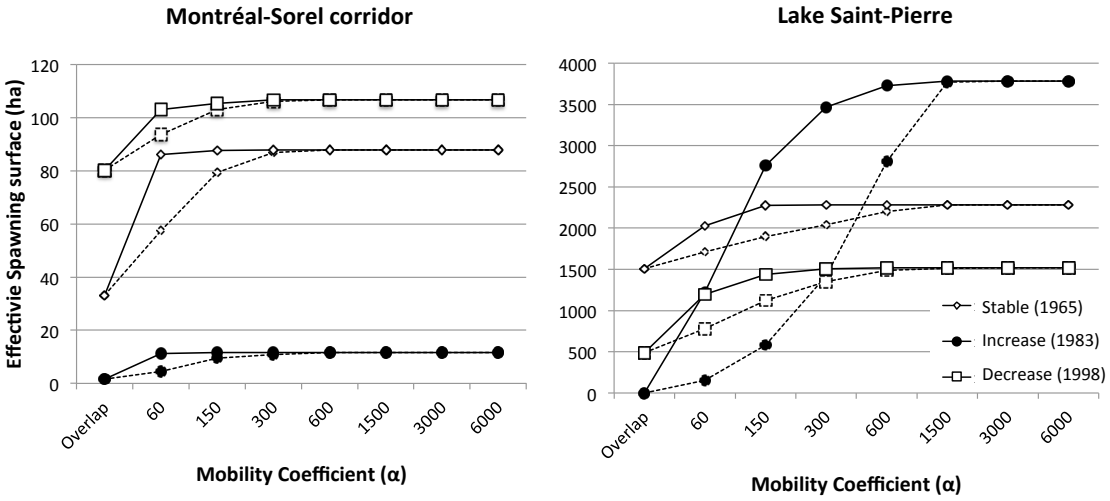

Figure 2.8 Relationship between effective spawning surface of northern pike and mobility coefficient (α) in the Montréal-Sorel corridor and the Lake Saint-Pierre of the St. Lawrence River for the three profiles (stable in 1965, increase in 1983, decrease in 1998). The solid lines represent the α as a distance integrating the minimal cumulative resistance (i.e. with downstream current facilitations) whereas the dotted lines represent the α equivalent to instream distance (i.e. without downstream current facilitations).

The capacity for larvae to move upstream against the current (<2 cm.s^{-1}) did not increase the overall area of effective spawning habitat by more than 2% in any simulations (e.g. for all three hydrological conditions and both regions). However, if the current speed threshold is increased from 10 cm.s^{-1} to 12 cm.s^{-1}, the total area of

effective spawning habitat increased by 5% in stable profile (1965), 11% in increasing profile (1983), and 3% in decreasing profile (1998) in the Lake Saint-Pierre and by 22% in stable profile, 78% in increasing profile and 3% in decreasing profile in the Montréal-Sorel corridor (appendix Figure B.3). When the threshold was fixed to 14 $cm.s^{-1}$, the increase in the area of effective spawning habitat was still significant in increasing profile for the corridor (increase of 84%).

2.5 Discussion

Our simulations demonstrate that (1) naturally, vast potential spawning areas are not connected to nurseries, this was exacerbated during profiles typified by large and rapid dewatering waters, (2) passive transport by current speeds is a key mechanism connecting uncoupled spawning and nursery habitats in a large fluvial lake especially during increasing flood profiles, (3) overlap between spawning and nursery habitats is favoured by stable hydrological conditions between spawning time ($Week_0$) and time larvae enter nurseries ($Week_5$) and, (4) habitat connectivity within ecologically-distinct regions, such as the fluvial lake and the riverine corridor studied herein, responded differently to spring water discharges conditions. This suggests the perceived potential provided by large and highly productive riverine ecosystem in generating effective spawning habitats is rather extremely variable both spatially and temporally.

2.5.1 The riverscape modelling

The least-cost approach coupled to habitat suitability modelling and hydrodynamic simulations, proves powerful for exploring the hydrological and biotic connectivity in heterogeneous and dynamic landscapes. Our spatially explicit model allowed us assessing early-life history dynamics over a 50-year period. This historical perspective unveiled spatially and temporally variable patterns of connectivity, an aspect virtually impossible to assess through *in situ* analyses.

Spawning and nursery habitat distribution predicted by the habitat models match sporadic field observations made over the last 30 years in unaltered SLR areas (e.g. Lavallière bay and Boucherville islands, Mingelbier et Leclerc 2001). The observed density of northern pike parallels the overall availability of potential habitats modelled; northern pike is more abundant in the Lake Saint-Pierre than in the Montréal-Sorel corridor (standardized governmental fish survey, described in La Violette *et al*. 2003). Moreover, several independent observations made on the SLR northern pike stocks revealed negative associations between northern pike year-class strength index and high variability in spring water levels (Smith *et al*. 2007; Hudon *et al*. 2009). Ouellet-Cauchon et al. (2014) correlated the lack of significant genetic population structure for northern pike in the SLR to the spatio-temporal variability in spawning habitats localization.

Although we considered that the most important habitat variables in the SLR (depth, current speed, vegetation and temperature) were considered in our HSI, more variables were known for their impact on eggs and larval pike survival such as pH, oxygen and predation (Siefert *et al*. 1973; Le Louarn et Webb 1998; Lehtiniemi 2005). We believe, if considered, these variables could improved our understanding of the spatio-temporal heterogeneity, however, since all these variables are considered as non-limiting in the present context, their contribution is not expected to modify significantly the present conclusions. Considering how Habitat Suitability Index (HSI) are calculated (a new variable cannot increase an HSI nor compensate for another deficient variable), including more variables can only exacerbated the spatial heterogeneity quantified by generating further areas of “unsuitability” (low HSI indices).

2.5.2 Spatial constraints on early-life habitat connectivity

2.5.2.1 Effective Spawning Habitat

Spatial overlap of spawning habitats and nursery areas has been reported to favor larval survival and growth in ecosystems characterized by high water discharge variations such as large rivers (e.g. Schiemer *et al*. 2003) and marine systems (e.g. Dickey-Collas *et al*. 2009; Ospina-Alvarez *et al*. 2012). In the SLR, when hydrological conditions allow large spawning areas to overlap nurseries, up to 1 507 ha and 80 ha of effective spawning habitats can be generated in the Lake Saint-Pierre and the Montréal-Sorel corridor respectively.

When spawning and nursery habitats are spatially disjunct, downstream current facilitation appears as a potent mechanism allowing the creation of large effective spawning areas by overcoming the absence of physical habitat overlap in the Lake Saint-Pierre. In marine ecosystems, passive transport of eggs and larvae by currents is considered as a key mechanism connecting spawning habitats to nursery areas (Werner *et al*. 1997; Hare *et al*. 2002; Hufnagl *et al*. 2013). The role of such mechanism has been highlighted recently in freshwater environments (Schiemer *et al*. 2003; Miehls et Dettmers 2011). Although drift could be seen a purely passive process, the larvae dispersal, even in low water currents, appears nevertheless associated to some energetic costs such as short burst of swimming activity (Peake 2004).

2.5.2.2 Non-Effective Spawning Habitat

Spawning habitats may turn into mortality traps through rapid environmental changes decreasing suitability of initially high-quality spawning habitat (e.g. Jeffres et Moyle 2012). Firstly, past studies have highlighted the vulnerability of pike eggs to a rapid dewatering after deposition (e.g. Johnson 1957; Dumont et Fortin 1977; Inskip 1982). Here we observed that decreasing water discharge over a period of five weeks, such as the conditions modelled for year 1998, drained 70% and 46% of potential

spawning habitat in the Lake Saint-Pierre and in the Montréal-Sorel corridor respectively. Secondly, water discharge fluctuations during early-life history stages may disperse larvae away from suitable habitats through critical current speeds, resulting in mortality (e.g. Heggenes et Traaen 1988; Rochette *et al*. 2012; Lechner *et al*. 2013). High current speeds turned into mortality traps 92% of potential spawning habitat areas in the corridor and up to 17% in the lake.

Physical barriers such as drained areas and fast current speeds can restrict the passive transport by currents and consequently the connectivity between spawning and nursery habitats. For example, larvae can be trapped in off-channel habitats (Bradford 1997) such as in the Lavallière bay of the Lake Saint-Pierre (located on Figure 2.1). Although unconnected on a seasonal basis, such habitats may provide refuges for some species (e.g. by reducing the possibility of encountering predators: Martens et Connolly 2014). The present results show that seasonally unconnected habitats dried out and acted as mortality traps for northern pike in the SLR. However, such phenomenon was not a major cause creating non-effective spawning habitats, they are responsible for only 1 to 6% of habitat losses.

2.5.3 Temporal variations of effective spawning habitats and hydrological conditions

The annual variability of hydrological conditions during springtime can transform entirely the connectivity between spawning and nursery habitats in the St Lawrence River. Although regularizing the Ottawa River (1912) and the Lake Ontario (1958) outflows has drastically reduced the springtime maximum water discharge (Morin et Bouchard 2000), the spring outflow from the major tributaries can still generate important hydrological variability between Montréal and Trois-Rivières. Consequently, the hydrological variability creates important variations in effective spawning habitat distribution and superficies available annually, which can explain

the northern pike recruitment variability documented in its vast river system (Smith *et al*. 2007; Hudon *et al*. 2009).

According to the flood pulse concept (Junk *et al*. 1989), a predictable long flood duration in the SLR can create large effective spawning habitat areas resulting in a potential high productivity in the aquatic/terrestrial transition zone. Stable water discharges during the five first weeks of the pike's ontogeny will favor almost automatically habitat overlap between spawning and nurseries habitats. This situation is explained by the similarity of the environmental conditions (e.g. current speeds <10 $cm.s^{-1}$, shallow water depth) leading to optimal conditions for both habitats (e.g. high Habitat Suitability Index). Consequently, stable early spring conditions, which are occurring 33% of the time in the SLR since 1965, has certainly contributed to northern pike recruitment success in past years. Nevertheless, the stability occurring at low or high water discharges may be associated to a different recruitment level. High water discharges may generate more extensive spawning and nursery habitat areas than low water discharges.

In contrast, a brief flood pulse, resulting in rapid decreasing or increasing water discharges between the spawning and nursery periods, will reduce the effective spawning areas through mortality traps. Even though decreasing water discharge occurred 53% of the time over the 1965-2013 period in the SLR, we predicted that spawning habitat area losses would not always be as high as in spring 1998 because reduction in water discharges were on average lower (i.e. 15,296 $m^3.s^{-1}$ to 11,532 $m^3.s^{-1}$ in 1998 versus 12,821 $m^3.s^{-1}$ to 11,481 $m^3.s^{-1}$ on average). On another hand, a rapid increase of water discharge, typified in our study by the year 1983, amplified the risk of larvae being washed off spawning habitat. Such a scenario occurred in 14% of the years covered by the 1965-2013 period. Nevertheless, it appears that even a slight increase in water discharge impacted spawning habitat

quality, but in this case the impacts are restrained almost exclusively the deeper margin of spawning habitats (e.g. 1965, Figure 2.7).

2.5.4 Two ecologically distinct regions

While the spatio-temporal heterogeneity of effective spawning habitats and the role of larval dispersal in the Montréal-Sorel corridor were more similar to the conditions observed in large fluvial channelize river, the situation observed in the Lake Saint-Pierre is quite different. The mechanisms controlling fish recruitment in the large Lake Saint-Pierre exhibit characteristics analogous to marine systems (Ludsin *et al*. 2014; Weber *et al*. 2015). The "ideal" hydrological conditions favoring the greatest effective spawning habitat superficies while minimizing the occurrence of mortality traps appeared quite different between the two contrasting, but longitudinally connected, ecosystems considered herein.

2.5.4.1 The Montréal-Sorel corridor

In large channel river systems such as the Montréal-Sorel corridor, steep banks and fast current speeds appears as limiting factor restraining (1) the spatial extend of spawning and nursery habitat areas, (2) larval dispersal to nursery habitat located only in short distances from the spawning habitat (Lechner *et al*. 2013), while (3) exacerbate the risk of larvae being washed off from either the system or nursery habitat reaches. High water discharge has been shown to reduce spawning and nursery habitat areas and increase their fragmentation in channel systems with steep banks (e.g. Tiffan *et al*. 2002; Le Pichon *et al*. 2009). A similar effect is observed in the Montréal-Sorel corridor, where medium water discharge remaining stable appear as the most suitable hydrological conditions favoring effective northern pike habitats. Nevertheless, effective spawning habitats appeared more aggregated and more fragmented along the narrow corridor than in the large fluvial Lake Saint-Pierre (Figure 2.6, Table 2.1; Mingelbier et Leclerc 2001). Habitat fragmentation favours

biological interactions such as competition and predation, which negatively influence the fish recruitment success (e.g. Nanami et Nishihira 2003).

2.5.4.2 The Lake Saint-Pierre

In marine systems, physical processes (e.g. currents and winds) are often regarded to prevail over biological interactions (e.g. predation) as the main explanatory factor of the recruitment success (Sinclair 1988). Although there are obvious differences between large fluvial lakes and marine systems, the prevalence of physical over biological factors on recruitment success, such as water discharge variations and downstream current facilitations, were suggested in the Lake Saint-Pierre. For example, even if the maximal transport distance was shorter than in marine systems (e.g. 20-30 km in 21 days; Basterretxea *et al*. 2012), the larval dispersal allowed larvae travelling up to 3,000 m in 7 days in the Lake Saint-Pierre is nevertheless five times higher than the range of 200-500 m observed in typical lentic lakes by Cucherousset *et al*. (2009) and Skov *et al*. (2011). This result suggests that recruitment processes may occur at broader spatial scales in energetically dynamic fluvial lakes compared to smaller freshwater lakes and streams. Nevertheless, transport patterns and the proportion of larvae reaching nurseries varied substantially among years in the Lake Saint-Pierre as in marine systems (e.g. Bolle *et al*. 2009). In fact, large and productive systems such as fluvial lakes and coastal regions (Soto-Mendoza *et al*. 2012; Sheaves *et al*. 2014) are now regarded as much more heterogeneous both spatially and temporally than what was reported earlier (e.g. Lake Saint-Pierre in Centre-Saint-Laurent 1996). Thus, high water discharges remaining stable seem to be more beneficial for maximizing recruitment in fluvial lakes, as they are generating large suitable habitat areas (Gorski *et al*. 2011) with important spatial overlap between spawning and nurseries habitats (see arguments above).

2.5.5 Implications for management

As pike stock decline has been often associated to habitat loss (e.g. Smith *et al*. 2007), restoring connectivity between remaining habitats can be a potent management solution. In the present study, the several facets of habitat connectivity impacting northern pike population dynamic revealed key elements that must be considered altogether to successfully restore habitat in a spatio-temporally variable river floodplain landscape.

Firstly, as potential spawning habitats may be not connected to a nursery area, focusing exclusively on spawning site, or alternatively on nurseries, could be misleading by suggesting that, once they are protected, they will automatically favour recruitment. Secondly, the habitat connectivity can rapidly change in space and time according to the hydrological regime. Modelling early-life history over a 50-year period can helps anticipating the spatio-temporal dynamic of the connectivity and identifying recurrent effective spawning habitats and nurseries to be protected in order to maximize investment dedicated to improve recruitment. Thirdly, factors and processes acting on the connectivity are different in ecologically distinct regions. Assessing the influence of the connectivity at larger scale (i.e. between regions) can be fundamental if the elevated productivity of a region can be exported to compensate for the recruitment failure in another neighbouring region (e.g. Jeffres et Moyle 2012).

Modelling the spatio-temporal distribution and extent of effective spawning habitats in an unaltered floodplain landscape reveal a surprising heterogeneity and variability despite the presumption that large, continuous, vegetated floodplain area should be adequate for pike spawning and recruitment. Considering that floodplains are under increasing pressure from various usage (Tockner et Stanford 2002), the actual situation prevailing in anthropised floodplain will be exacerbated. Indeed, human activities, such as intensive agriculture practices, alters natural habitats and impede

floodplain connectivity (e.g. Fernandes *et al*. 2015). Because of all the various components required for a species to successfully recruit in an ecosystem, which are magnified during the first stages of the life cycle, local alterations created in a dynamic landscape as multiple chances in creating adverse conditions. Only one of either, the spawning habitat, the connectivity (e.g. areas allowing drift, current speed, etc.) or the nursery habitat quality had to be impacted to render unproductive previously naturally-suitable areas. In this perspective, unaltered landscape models can be used as a blueprint to compare the dynamic prevailing in pristine landscape to contemporary, altered, state. Such comparisons can (1) highlight areas the most rewarding to be targeted by managers, (2) allow identifying which component ought to be restored to maximise recruitment potential provided by the existing spawning biomass (e.g. spawning habitats, nurseries, connectivity) and (3) to implement new management rules protecting key areas or process favoring recruitment in spatio-temporally variable landscape.

2.6 Acknowledgments

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CHAPITRE III

EFFECTIVE FISH SPAWNING HABITATS IN ANTHROPISED FLOODPLAIN ECOSYSTEMS : THE PARADOX OF THE MOST PRODUCTIVE YEARS

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In preparation for *Landscape Ecology*

3.1 Abstract

The hydrological and land-use modifications in floodplain ecosystems have resulted in habitat losses and further landscape fragmentation, translating in profound changes in riverine patterns, including fish communities' productivity and diversity. In the fluvial Lake Saint-Pierre (St. Lawrence River, Canada), we investigate how water flow regulation and agriculture have impacted effective spawning habitats of northern pike (*Esox lucius*). An analysis of land-use changes, coupled to habitat and connectivity modelling, was conducted in this vast fluvial lake for the period covering 1965 to 2013. We quantified how changes in agriculture practices led to significant habitat losses during years of high and stable water discharges, such years being considered as driving productivity patterns (i.e. favouring recruitment) since they are theoretically the most productive years for floodplain spawners. Moreover, we stressed that water regulation in the St. Lawrence River, and especially through the Ottawa River (its main tributary), have reduced the connectivity between pike's

spawning and nursery habitats. These two combined effects, resulting in a general lowering of production potential of the Lake Saint-Pierre, have created a *paradoxical* situation. High water discharges are now associated to a lower productive potential than low water discharges. While all the spawning habitat area generated during low water discharges are almost all effective in favouring larval survival, most of potential habitats generated during high water discharges are lost through rapid dewatering and the alteration of habitats resulting from agricultural practices. Such situation occurred more frequently in the St. Lawrence River since its regularisation. These findings suggest the necessity to restore habitats by converting agriculture crops located in the floodplain, and assessing the possibility to restore a more natural profile of water discharge variations. Moreover, we identified and localised the most recurrent high-quality spawning habitats that offers the most rewarding areas to be protected. In addition, we found that existing drainage ditches could be used to enhance the connectivity network within the floodplain.

Keywords: northern pike, agricultural landscape, water regulation, least-cost modelling.

3.2 Introduction

The floodplain is a dynamic aquatic-terrestrial interface of lowland rivers. It plays an important role by providing a mosaic of effective spawning habitats from which fish may recruit to the adult population (Bayler 1991; Gorski *et al*. 2011). However, floodplains are under increasing anthropogenic pressure around the world (Tockner et Stanford 2002). The impacts of water flow regulation and the expansion of agriculture are major threats for the floodplain ecosystems (Beesley *et al*. 2014; Fernandes *et al*. 2015), where potential spawning habitats can be transformed in mortality traps (e.g. Jeffres et Moyle 2012; Sheaves *et al*. 2014). Quantifying the effects of anthropogenic pressures on effective spawning habitats allows identifying large-scale environmental disturbances behind widespread recruitment failures (e.g.

Goto *et al*. 2015), an important prerequisite for restoring and managing floodplains ecosystems.

Water flow regulations creates substantial changes in hydrological regimes in many river systems worldwide, which can be critical for the overall production of riverine fish (Nilsson *et al*. 2005). The hydrological regimes in floodplains (i.e. magnitude, duration and the periodicity of water levels) are highly variable in space and time, which in turn exert a major driving force on habitat surfaces available and on landscape connectivity (Junk *et al*. 1989; Wiens 2002). Although extensive areas flooded for long duration can improve the recruitment success of riverine fish, a rapid decrease of water discharge early in the life of fish may suddenly dewater or isolate spawning habitats, resulting in egg and larvae mortality (Bayler 1991; Gorski *et al*. 2011).Thus, hydrological modifications can alter severely the quality of riverine habitats and riverscape features acting as physical barriers. The reduction of maximal water discharges, for instance, are limiting the surface of spawning and nursery habitats available that can be result in the steady decline of riverine fish population of several major river systems (e.g. Goto *et al*. 2015). In addition, the man-made hydrological conditions allowed settlement in the floodplains and further developments of human activities.

Extensive natural floodplains area converted to agriculture resulted in net loss of fish habitats (Baber *et al*. 2002), a reduction in fish eggs and larvae abundance (Matsuzaki *et al*. 2011), and jeopardised the long-term persistence of several fishes (Fernandes *et al*. 2015). In addition, transportation infrastructures such as roads along rivers may disconnect significant portion of the floodplain extent, reducing the access to vital habitats (Blanton et Marcus 2014). Consequently, species have to travel longer distances to reach spatially disconnected suitable habitats. As larval fish exhibit limited swimming capacities, passive transport using low water current speeds (Schiemer *et al*. 2003) and landscape features such as ditches network (Washitani

2007) may facilitate larval dispersal, such alternative use of man-made structure may contribute to maintain floodplain connectivity in an anthropised landscape.

In the present study, we explore how hydrological and land-use changes have impacted the effective spawning habitats in the spatio-temporally heterogeneous landscapes of the fluvial Lake Saint-Pierre floodplain (St. Lawrence River, Canada). We used as a model species the northern pike (*Esox lucius*), an archetypal early-spring spawner in the floodplain. During the last decades, northern pike has declined in several large river systems (Boët *et al*. 1999; Raat 2001) including the St. Lawrence River. In several cases anthropogenic pressures are pointed out for their role in the actual stocks' dismal status. In the course of the 20th century, as water flow became regulated and extensive agricultural practices developed, we estimated that natural habitats and connectivity steadily became altered.

Specifically, potential northern pike spawning and nursery habitats were simulated in the unaltered landscape of the Lake Saint-Pierre (Foubert *et al*. in prep, see chapter II in the present thesis) for the period covering 1965-2013 and then compared to the contemporary altered state. Historical analysis were performed to (1) assess the progressive losses of habitats from agriculture since 1965 and (2) identify the best recurring habitats during a 49 years period. In addition, contrasting conditions representing the hydrological variability in the St. Lawrence River were selected to (3) test the effects of water depth, current speed, dense vegetation, roads, drained ditches and channelized stream on connectivity between spawning and nursery habitats and to (4) quantify the loss of fish habitat created by contemporary land-use that renders unsuitable previously effective spawning habitats. Finally, the current hydrological regime, which has been regulated in successive steps, was compared to the period preceding water flow regulation to assess its impacts of potential fish production.

3.3 Methods

3.3.1 Study area

The Lake Saint-Pierre is the largest fluvial lake of the St. Lawrence River (SLR; Figure 3.1). This river system is one of the largest of the world both in terms of watershed area (1,344,200 km^2) and mean annual discharge (10,270 $m^3.s^{-1}$ at Sorel, Morin et Bouchard 2000). The Lake Saint-Pierre and its associated archipelago were listed in 2000 as a UNESCO Word Heritage Biosphere. The gentle lateral bottom slope (depth <3 m) combined with slow-flowing (current speeds <0.5 $m.s^{-1}$) and extensive macrophyte beds (Centre-Saint-Laurent 1996) make this lake look like a gigantic marshland. The interannual variability of spring water discharges, ranging between 6,500 and 17,500 $m^3.s^{-1}$ at Sorel, is a key mechanism maintaining floodplain wetlands vegetation (Morin *et al*. 2005).

Since the beginning of the industrial era, cumulative anthropogenic pressures have altered the Lake Saint-Pierre ecosystem. Water-regulation of the SLR began in 1911 with the harnessing of its main tributary for hydropower generation, flood control and navigation: the Ottawa River. The regulation of the SLR was further push forward by the completion of the Moses-Saunders and Beauharnois Power Dams controlling the Lake Ontario – SLR system in 1958. Moreover, a deep navigation channel divides the river transversally (width ≥300 m; depth ≥11.3 m; mean current speed of 0.5-2.0 $m.s^{-1}$); no water exchange occurs between the north and the south shores. Several water masses are flowing side-by-side without mixing in the portion upstream of Trois-Rivières (Frenette *et al*. 2006; Hudon et Carignan 2008). In addition, major urban areas (e.g. Montréal, Trois-Rivières, and Québec City), intensive agriculture, and transportation infrastructures located along the SLR have severely impacted the fish habitat. Over time, perennial crops (e.g. pasture), which are used successfully as fish habitat, were replaced by annual crops (e.g. corn, soya)

with no potential for fish; this phenomenon has accelerated since the beginning of the 1990's (Fecteau et Poissant 2001; de la Chenelière *et al*. 2014).

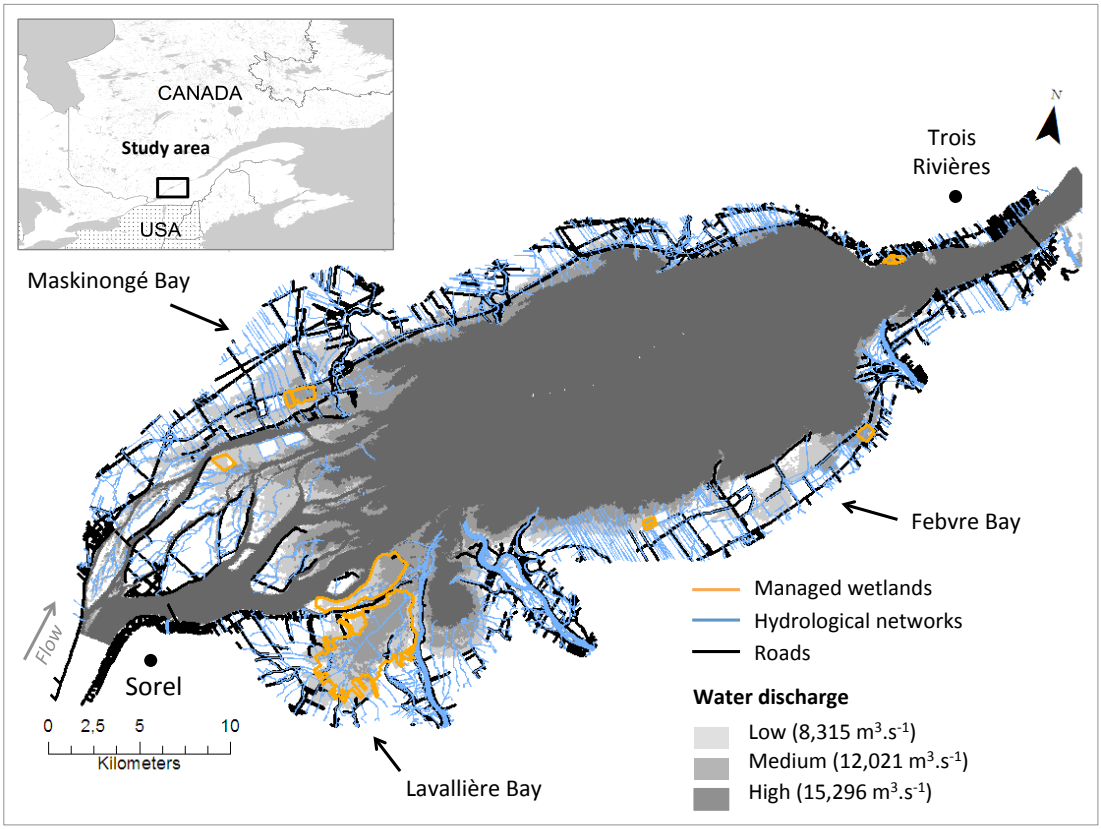

Figure 3.1 Map showing the largest fluvial lake of the St. Lawrence River: the Lake Saint-Pierre and its archipelago (Québec, Canada). Fish managed wetlands, hydrological networks (drained ditches and channelized streams) and roads on the floodplain were localised. Flooding surfaces of three contrasted spring water discharges (low, medium, high) were presented.

3.3.2 Potential habitats modelling (1965-2013)

Spatially explicit models developed by Environment Canada (Morin et Bouchard 2000; Turgeon *et al*. 2004; Morin *et al*. 2005) were used to simulate Habitat Suitability Indices (HSI) for northern pike spawning habitats at the maximal

spawning time ($Week_0$; developped in Mingelbier *et al*. 2008a) and nursery habitats five weeks later at the beginning of free-swimming stage ($Week_5$; Foubert *et al*. in prep, see chapter II in the present thesis). Spatially explicit models are based on a dense simulation grid with a node every 40 m. Each node supports local physical variables such as water depths, current speeds, wetland types and potential water temperatures on a weekly resolution for the period covering 1965 to 2013. The model simulating the extent of flooding and the succession of natural wetlands was calibrated using field observations (Morin et Bouchard 2000).

3.3.3 Land-use description

Land-use in the Lake Saint-Pierre floodplain was described using aerial photographs in 1964 and 1997 (Richard *et al*. 2011), and through satellite imagery in 2014 (Jobin et Dauphin in prep). In the present study, we interpreted the various land-use types and assigned land use to six categories from the most suitable to the least suitable for fish habitats: (1) suitable wetlands for spawning and nursery habitats (e.g. wet meadow and marshes), (2) drainage ditches and channelized streams (the main network), (3) perennial crops (e.g. pasture and forage crops), (4) unsuitable wetlands and wooded areas (e.g. wooded peat-bogs and plantation), (5) roads and urban areas, and finally (6) annual crops (e.g. wheat and soya) (see all land-use types and their associated categories in appendix Table C.1). While suitable wetlands, perennial crops and drainage ditches categories are suitable for fish habitats, unsuitable wetlands and wooded, annual crops, and roads and urban areas categories have negatively altered the fish habitats in the Lake Saint-Pierre floodplain. Only one land-use type differs between the categories used for spawning and nursery habitats: we considered treed swamps suitable wetland for nurseries (e.g. food supply) while unsuitable for spawning as a result of the lack of appropriate substrate for eggs deposition. In addition to these six categories, the localisation of managed wetlands used for fish production was included (Mingelbier et Douguet 1999 updated with field observations: see Figure 3.1). With theses information, we can assess the role of

managed wetlands in maintaining effective spawning habitats in the Lake Saint-Pierre floodplain.

Several landscape features included in the land-use description may restrict or facilitate landscape connectivity and larval movements. We considered that roads, managed wetland dykes and dense suitable wetlands restrict connectivity whereas drained ditches and channelized streams are facilitating connectivity. As a consequence of hydrological variability observed in floodplain areas, we differentiated submerged roads/dikes that do not restrict the connectivity of emerged roads/dikes that restrict the connectivity by overlapping the land-use description, simulated water depths and LiDAR data. The accuracy of topographic measurements (every meters) provided by LiDAR allowed us identifying submerged and emerged elements for contrasted hydrological conditions in the lake. Moreover, permanent structures (i.e. culverts, water control structures and weirs) allowing larvae to cross roads and dykes were identified using published material (Mingelbier et Douguet 1999), field observations and geomatic treatments. When a road intersects a ditch or a river, a culvert has been considered. Finally, wet meadow and shrubby swamps located in a simulated water depth <20 cm creating dense suitable wetlands are nevertheless acting as physical barriers to dispersal (named hereafter dense vegetation).

3.3.4 Historical analysis

3.3.4.1 Agriculture and altered habitats

Spawning ($HSI_{spawning}$) and nursery ($HSI_{nursery}$) habitats loss to agriculture (i.e. soya, corn, wheat, vegetable crops, oat, barley, other cereals) was calculated annually. As the extent of annual crops progressively increased between the three land-use descriptions (i.e. 1964, 1997 and, 2014), we realised a linear interpolation using these three references to estimate habitat area losses early between 1965 and 2013. Spearman's Rank Correlation Coefficient was used to evaluate (1) the relationship

between the total potential spawning habitat lost with the annual agricultural crops and water discharge at the moment of spawning ($Week_0$) and (2) the relationship between the total potential nursery habitat lost with the annual agricultural crops and the water discharge when larvae became free-swimming ($Week_5$).

3.3.4.2 Spatial recurrence of habitats

To assess the effect of hydrological variability on spatial distribution of habitats, spatial recurrences of $HSI_{spawning}$ and $HSI_{nursery}$ were calculated for the period covering 1965-2013. Recurrences were pooled into four classes: habitats recurrent every year during the 49 years period, every 2 years, every 4 years and over every 10 years. Then, maps were overlaid to the contemporary land-use description (i.e. 2014) to evaluate potential habitat losses generated by unsuitable land-use categories (i.e. unsuitable wetlands and wooded, annual crops, and roads and urban areas).

3.3.5 Hydrological analysis

3.3.5.1 Hydrological conditions selected

Since hydrological regime was variable during the period studied (1965-2013), water discharge between the maximal spawning time ($Week_0$) and the free-swimming stage ($Week_5$) can be classified to four distinct profiles[1] (1) stable low, (2) stable high, (3) increasing, and (4) decreasing. We therefore selected four years between 1965 and 2013 representing each one of the four profiles to assess their influence on pike's springtime spawning dynamics (Table 3.1): the year (1) 1965 corresponded to low but stable water discharges between $Week_0$ and $Week_5$, (2) 1973 corresponded to high and stable water discharge between $Week_0$ and $Week_5$, (3) 1983 corresponded to an "average" discharge at $Week_0$ increasing toward $Week_5$; and (4) 1998 corresponded to a high water discharge at $Week_0$, decreasing at $Week_5$. Historical analysis covering

[1] En comparaison au chapitre II de la présente thèse, un profile stable avec un niveau d'eau haut

the 1965 to 2013 period revealed that recurrences of the four profiles are 16%, 16%, 14% and 53% respectively (Foubert *et al*. in prep, see chapter II in the present thesis).

Table 3.1 The total surface of habitats and the total number of patches for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998) were calculated for potential spawning habitats at the maximal spawning time ($Week_0$; developed in Mingelbier *et al*. 2008a) and nursery habitats five weeks later at the beginning of free-swimming stage ($Week_5$; Foubert *et al*. in prep, see chapter II in the present thesis) in the Lake Saint-Pierre (St. Lawrence River, Canada).

Years	Water discharge ($m^3.s^{-1}$)	Profile	Flooded surface (ha)	Habitat surface (ha)	Number of patch
1965					
Spawning habitats - $Week_0$	Low (8,315)	Stable	41,768	**2,794**	253
Nursery habitats - $Week_5$	Low (8,455)		44,731	**5,107**	459
1973					
Spawning habitats - $Week_0$	High (14,853)	Stable	57,800	**5,242**	369
Nursery habitats - $Week_5$	High (14,920)		58,868	**5,047**	718
1983					
Spawning habitats - $Week_0$	Medium (12,021)	Inscrease	49,455	**4,608**	311
Nursery habitats - $Week_5$	High (14,905)		62,099	**5,277**	751
1998					
Spawning habitats - $Week_0$	High (15,296)	Decrease	59,407	**6,045**	347
Nursery habitats - $Week_5$	Medium (11,532)		46,551	**3,019**	502

3.3.5.2 Connectivity estimates

A least-cost approach to model movement within landscapes (Adriaensen *et al*. 2003) was used to quantify connectivity between spawning habitat at the maximum spawning time ($Week_0$) and nursery habitat at the beginning of the free-swimming stage ($Week_5$). In this approach, every landscape features are assigned to a 'resistance' value according to its restricting/facilitating effects on animal movements

(i.e. Minimal Cumulative Resistance concept) for either upstream and downstream directions (e.g. Caldwell et Gergel 2013; Hanke *et al*. 2013; Roy et Le Pichon 2017).

We assigned a resistance value to landscape features simulating the mortality risk or the difficulty of traversing the landscape when moving out of spawning habitats. Firstly, landscape environmental features sensitive to hydrological variations were considered. Resistance values were adapted from Foubert *et al*. (in prep, see chapter II in the present thesis); they allow assigning to each point (or pixel) of the landscape the combined effects of water discharge and current speeds on egg survival and larval dispersal (see Table 3.2). In the present study, we considered the dense vegetation as an environmental feature of the landscape. A maximum resistance value preventing any survival or successful dispersal was assigned to dense vegetation. Secondly, anthropic features restricting (i.e. exposed roads) or facilitating (i.e. drained ditches and channelized streams) dispersal within the landscape were also considered. A resistance value of 1 involves unaided upstream and downstream movements (i.e. only larval swimming capacity is considered) was assigned to drained ditches and channelized streams, whereas a maximum resistance value was assigned to exposed roads (e.g. larvae can't cross them). Others anthropic features observed in the contemporary landscape (e.g. agriculture) were not considered for connectivity estimates as they are believed not entirely restricting connectivity, or leading to mortality.

Table 3.2 Dimensionless resistance values based on the restricting/facilitating effects of all landscape features on the connectivity in either downstream or upstream directions. The water depth, current speed, drained ditches, exposed roads and dense vegetation are simulated during the beginning of free-swimming stage ($Week_5$). The water depth corresponds to the dewatering occurring between the spawning time ($Week_0$) and the free-swimming stage ($Week_5$) in the Lake Saint-Pierre.

Landscape feature		Downstream resistance value	Upstream resistance value
Water depth ≤ 0 m		10,000	10,000
Current speeds ($cm^3.s^{-1}$)	Speed > 0 ≤ 2	1	1
	Speed > 2 ≤ 4	0.3333	10,000
	Speed > 4 ≤ 6	0.2000	10,000
	Speed > 6 ≤ 8	0.1429	10,000
	Speed > 8 ≤ 10	0.1111	10,000
	Speed > 10	10,000	10,000
Drained ditches and chennalized streams		1	1
Exposed roads		10,000	10,000
Dense vegetation		10,000	10,000

Then, we used the *Anaqualand 2.0* freeware (Le Pichon *et al*. 2006a) to combine distance and resistance of landscape features generating the functional distance from spawning habitats to nurseries (see the method in Foubert *et al*. in prep, see chapter II in the present thesis [2]). The mobility coefficient (α) is a measure reflecting the functional distance allowed to be travelled by larvae across landscape. The coefficients are derived from stage-specific larval swimming capacities and potential passive transport provided by local currents at the beginning of the free-swimming stage ($Week_5$). The maximal value was set to α =6,000 m which corresponds to the maximal distance travelled at 1 $cm.s^{-1}$ by a neutral particle in the water column over a

[2] Figure 2.3 et appendices Figure B.1, Table B.1

period of one week in the SLR (see sensitivity analysis in appendix Table C.2, Figure C.1 and C2). Since α is a distance integrating the functional distance, it does not correspond directly to a physical instream distance. For example, a functional distance of 6,000 correspond to a distance of 600 m if the landscape feature is ten times more resistant (restrict the connectivity) or will correspond to a distance of 12,000 m if the current speeds disperse the larvae at twice the speed for a whole week.

3.3.5.3 Connected and disconnected spawning habitats

When the functional distance between a spawning habitat to a nursery is ≤ 6000 m $_{functional}$ (i.e. the maximal mobility coefficient), the spawning habitat is considered to be connected. In contrast, when the functional distance exceeded 6,000 m $_{functional}$, the spawning habitat is considered as disconnected. Connected and disconnected spawning habitats were mapped in *ArcGIS 10.1* and quantified (surface expressed in ha) for the four hydrological profiles. The gain or the loss of connected spawning area observed when each landscape feature is added (i.e. water depth, current speed, dense vegetation, drained ditches, and exposed roads) was also quantified (ha).

Moreover, the effects of landscape features restricting connectivity (i.e. water depth, current speed, roads and dense vegetation) were estimated. Direct losses correspond to potential spawning habitats spatially overlaid to landscape features. Technically, spawning habitats were overlaid to landscape features in *ArcGIS 10.1* to distinguish (1) spawning habitats lost to dewatering occurring between $Week_0$ and $Week_5$ (water depth ≤0, Table 3.2) from (2) spawning habitats lost because of an increase of current speeds (>10 $cm.s^{-1}$), or (3) exposed roads, or (4) dense vegetation. Indirect losses correspond to potential spawning habitats not connected to a nursery through landscape features acting as physical barriers impeding larvae dispersal.

3.3.5.4 Effective and non-effective spawning habitats

The total area of connected spawning habitats (i.e. including the effects of water depth, current speed, dense vegetation, drained ditches, and exposed roads) was overlaid to the six land-use categories of the contemporary description (i.e. 2014) in *ArcGIS 10.1*. It allowed us to quantify and differentiate the surface area of (1) remaining effective spawning habitat, which correspond to connected habitats overlap with suitable land-use categories (i.e. suitable wetlands, perennial crops and drainage ditches), and (2) the surfaces lost to anthropogenic alteration, which are connected habitats rendered unsuitable as they are located over inappropriate land-use categories (i.e. unsuitable wetlands and wooded, annual crops, and roads and urban areas). Finally, effective spawning habitat areas calculated for the four hydrological profiles (i.e. stable-low, stable-high, increasing and decreasing water discharges) were spatially overlaid to identify the most recurrent habitats.

3.4 Results

3.4.1 Historical analysis

3.4.1.1 Agriculture and altered habitats

As a consequence of agricultural intensification since 1965, up to 2,446 ha of potential spawning habitats and 1,188 ha of potential nursery habitats were lost in the Lake Saint-Pierre floodplain (see Figure 3.2). The annual agricultural impacts were particularly severe since 1990, since then the total spawning habitats did not exceed 5,500 ha.

The total loss of the two potential habitats modelled, either spawning or nurseries, was positively correlated with water discharges at $Week_0$ and $Week_5$ for spawning and nursery habitats respectively (the two *P*-value are <0.05, Spearman's rank correlation). While agricultural practices did not impact potential spawning and nursery habitats when low water discharges occurred, water discharge >14,000 $m^3.s^{-1}$

generated the largest loss of spawning and nursery habitats areas (Figure 3.2, appendix Figure C.3).

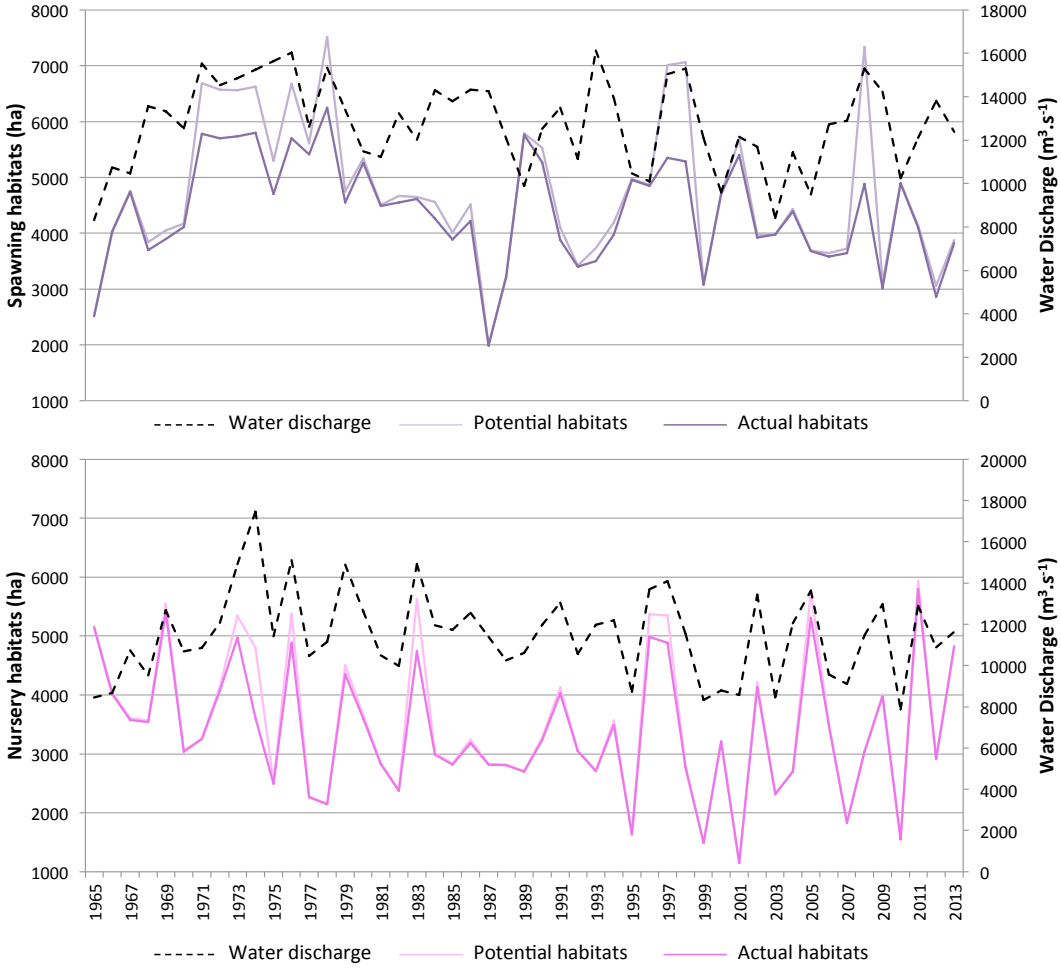

Figure 3.2 Temporal values of northern pike spawning and nursery habitats reconstituted for the period 1965-2013 in the unaltered (without agriculture) and the contemporary landscape (with agriculture) of the Lake St-Pierre (St. Lawrence River, Canada). Potential spawning and nursery habitat surfaces (left y-axis) in the unaltered landscape were adapted from Mingelbier *et al*. (2008a) and Foubert *et al*. (in prep, see chapter II in the present thesis) respectively. Actual spawning and nursery habitat surfaces include the losses generated by annual agricultural practices (i.e. the contemporary landscape). The water discharge (right y-axis) is measured during the spawning time ($Week_0$) and five weeks later at the beginning free-swimming stage ($Week_5$).

3.4.1.2 Spatial recurrence of habitats

As a consequence of hydrological variability observed since 1965, location of nursery habitats is less recurrent than location of spawning habitats (Figure 3.3). While only 0.003% (1 ha) of nursery habitats were located at the same site every two years, almost 21% (3,286 ha) of spawning habitats, all located along the shallow water fringe of the lake, were located at the same site every two years (black habitats in Figure 3.3). The spawning and nursery habitats altered by the land-use were located at the same site every four or more years during the 49 years period (light grey habitats in Figure 3.3). The annual agriculture explained the majority of spawning (62%) and nursery (87%) habitat loss.

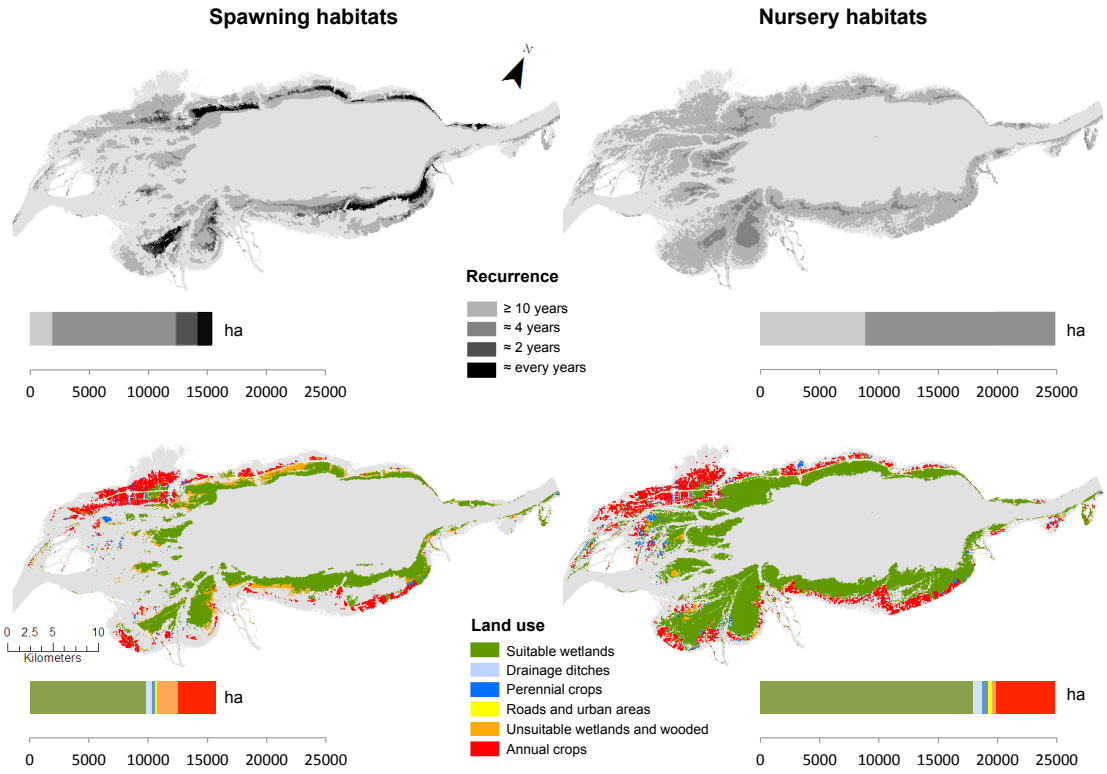

Figure 3.3 Spatial recurrences of potential spawning and nursery habitats during the period 1965-2013 in the Lake Saint-Pierre (St. Lawrence River, Canada). Recurrences were pooled into four classes: habitats recurrent every years during the 49 years period, every 2 years, every 4 years and more than every 10 years. Then, recurrences were overlaid to the contemporary land-use categories (description in 2014). While suitable wetlands, perennial crops and drainage ditches land-use categories are suitable for fish habitats, unsuitable wetlands and wooded, annual crops, and roads and urban areas categories have negatively altered the habitats in the Lake Saint-Pierre floodplain.

3.4.2 Hydrological analysis

3.4.2.1 Potential habitats

The total surface of potential spawning and nursery habitats available annually was driven by hydrological conditions (Table 3.1, Figure 3.4). High water discharges resulted in a large area of potential spawning (1998) and nursery habitats (1983), while low water discharges led to the smallest areas of spawning habitats (1965) and medium water discharges led to the smallest areas of nursery habitats (1998). Medium or high water discharges were sufficient to submerge managed wetlands located in the upper part of the floodplain. These high-productivity areas generating up to 571 ha and 722 ha of potential spawning and nursery habitats respectively. Moreover, the number of both habitat patches increase when water discharge is high (Table 3.1).

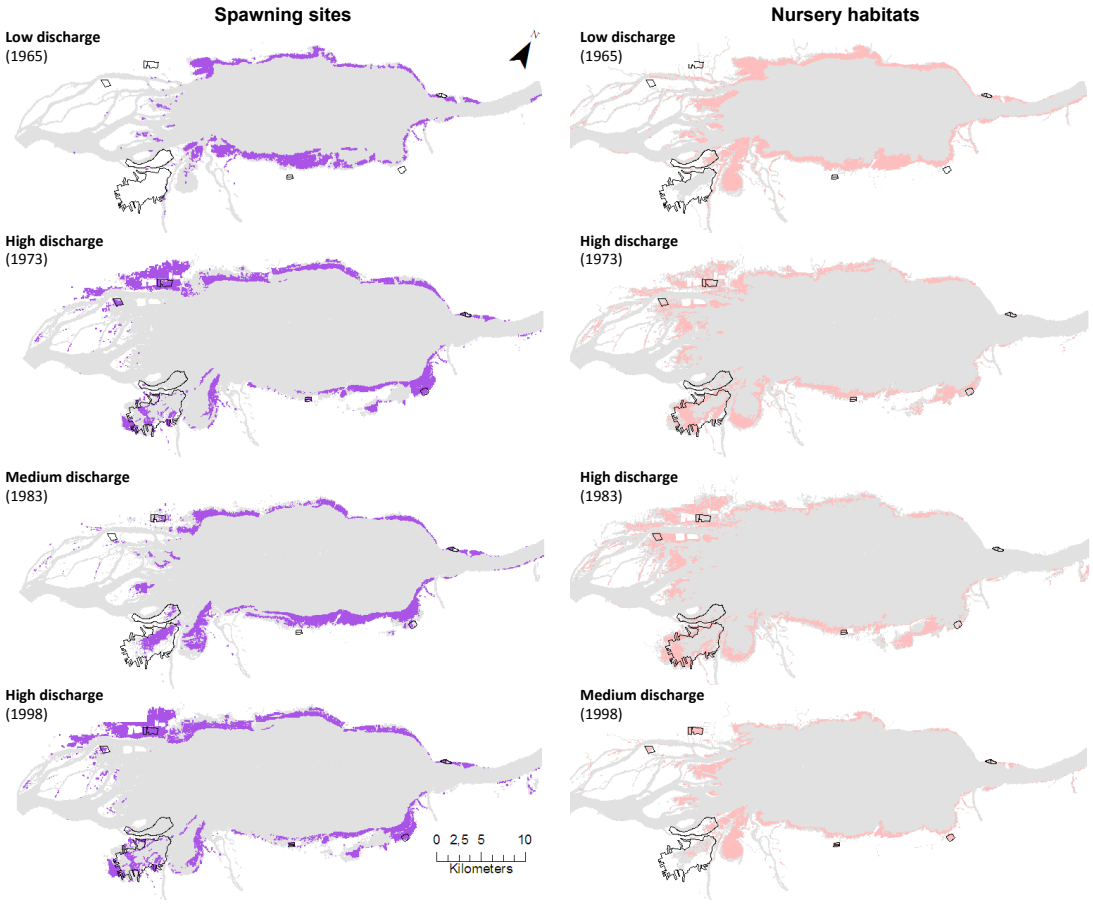

Figure 3.4 Map of the Lake Saint-Pierre showing potential spawning and nursery habitats of the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998). Fish managed wetlands (black outlines) generated potential habitats when medium-high water discharges occurred.

3.4.2.2 Connected spawning habitats

As a consequence of environmental (i.e. water depth, current speed, dense vegetation) and anthropic (i.e. exposed roads) features on habitat connectivity, 8 to 68% of potential spawning habitat were lost to recruitment as eggs did not survive or eithers larvae were unable to reach nurseries (Table 3.3). Firstly, the largest disconnected spawning areas appeared during a decreasing profile between the maximum spawning

time ($Week_0$) and the free-swimming stage ($Week_5$) as a consequence of dewatering 62% of potential spawning habitat area (1998). Secondly, increasing water currents above the 10 $cm.s^{-1}$ thresholds after spawning transformed high-quality habitats into low-quality habitats. These conditions appeared frequently during increasing profile (1983). Such fast water currents acting as physical barrier impeded access to 2% of spawning habitats during a stable-high profile (1973). Thirdly, dense vegetation slightly reduced the total surface of potential spawning habitats during a stable-high profile (1973), and acted as a physical barrier during a decreasing profile (1998). Fourthly, exposed roads altered spawning habitats when high water discharges occurred (i.e. spawning habitats are located in the upper part of the floodplain): 2% of potential spawning habitats were lost in 1973 and 1998. Even if the spawning habitat losses were low, exposed roads acted also as physical barriers during a stable-high profile (1973).

Table 3.3 Effects of landscape features that restrict the connectivity (i.e. water depth, current speed, roads and dense vegetation) on potential spawning habitat losses for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998) in the Lake Saint-Pierre (St. Lawrence River, Canada). The connected spawning habitat area is the result of a subtraction between the potential spawning habitat area (Habitat Suitability Indices) and the total habitat losses.

Profile (Years)	**Potential spawning habitats (ha)**	**Direct losses** (i.e. transform high to low habitat quality)					**Indirect losses** (i.e. act as physical barriers)				**Connected spawning habitats (ha)**
		Dewatered areas	High speeds (>10 cm.s^{-1})	Roads	Dense wetlands	**Total** (ha - %)	High speeds (>10 cm.s^{-1})	Roads	Dense wetlands	**Total** (ha - %)	
Stable-low (1965)	**2,794**	4	223	2	0	**229** [8%]	5	0	0	**5** [0.2%]	**2,560**
Stable-high (1973)	**5,242**	51	262	100	26	**439** [8%]	110	28	0	**138** [3%]	**4,665**
Increase (1983)	**4,608**	2	772	8	0	**782** [17%]	82	0	0	**82** [2%]	**3,744**
Decrease (1998)	**6,005**	3,758	61	117	66	**4,002** [66%]	72	0	25	**97** [2%]	**1,906**

When considering the effect of landscape features on habitat connectivity, the largest area of connected spawning habitat occurred during a stable-high profile (1973). This situation is possible thank to the overlap between spawning and nursery habitats, and to the larvae mobility coefficient (α =6,000 $m_{functional}$) that connected large spawning surfaces to distant large nursery areas (Figure 3.5). Potential spawning and nursery habitats physically overlapped created large areas of connected spawning habitats, this is especially true when water discharge remains stable between $Week_0$ and $Week_5$. Areas of habitat overlapping reached 55% of the total effective spawning area in a stable-low profile (1965) and 28% in a stable-high profile (1973), while 0.2% in an increasing profile (1983) and 10% in a decreasing profile (1998) were overlapped (see dark blue in Figure 3.5). Moreover, larvae mobility coefficients (α) allowed reaching distant nursery habitats specifically when (1) few spawning and nursery habitats were overlapped, and (2) when hydrological conditions maintained large spawning areas during the five first weeks of the ontogeny and generated large nursery area (see light blue in Figure 3.5). The larvae mobility (α) increased to 61% and 81% the area of connected spawning habitat during stable-high or increasing profiles respectively (1973 and 1983). When less spawning habitat areas are available at the beginning of free-swimming stage ($Week_5$), larvae mobility (α) increased to 36% (1965) and 21% (1998) the area of connected spawning habitat. Interestingly, during decreasing profile (1998), ditches and channelized streams located in drained areas allowed to further increase by 14% (252 ha) the surface of connected spawning habitats if larvae were able to move (see sensitivity analysis in appendix Table C.2, Figure C.1 and C2). Finally, managed wetlands are generating 463 ha of connected spawning habitat area during stable-high profile (1973), 439 ha during increasing profile (1983) and 216 ha during decreasing profile (1998).

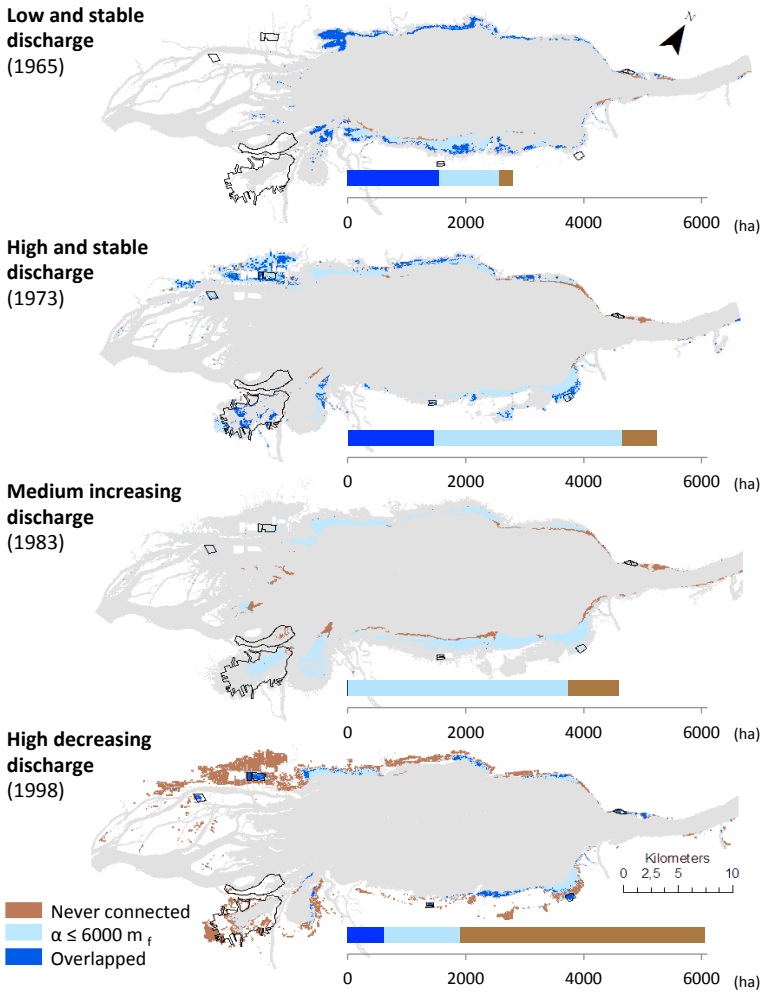

Figure 3.5 Map of the Lake Saint-Pierre showing disconnected and connected spawning habitats for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998) considering all landscape features (i.e. water depth, current speeds, drained ditches, roads, dense wetlands). Connectivity values correspond to three classes: (1) spawning habitats overlapping with nurseries (dark blue color), (2) spawning habitats connected when $\alpha \leq 6000$ m $_{functional}$ (medium blue color), and (3) spawning habitats which were never connected to any nursery (functional distance > 6000 m $_{functional}$; brown color). As α is a distance integrating the minimal cumulative resistance (i.e. functional distance), the α unit is not equivalent to instream distance (i.e. international metric system).

3.4.2.3 Effective spawning habitats

As a consequence of the contemporary land-use (i.e. 2014 description), zero to 47% of connected spawning habitats were transformed in low-quality habitats by unsuitable land-use categories (Figure 3.6). The largest connected spawning area losses were observed during a stable-high profile (1973) since 32% of habitats were directly render unsuitable by agricultural practices, mostly corn-soya crops. When water discharges reached medium (~11,000 $m^3.s^{-1}$) to high (~15,000 $m^3.s^{-1}$) discharges during the five first weeks of the ontogeny (i.e. in 1973, 1983 and 1998), unsuitable wetlands and wooded areas reduced by 11% to 14% the surface of connected spawning area. In addition to the habitat losses generated by exposed roads (see connectivity estimates; Table 3.3), less than 1% of connected spawning area was lost due to the presence of submerged roads and urban areas under any given hydrological conditions. Finally, only 0.4% of connected spawning area was impacted by the land-use during a stable-low profile (1965).

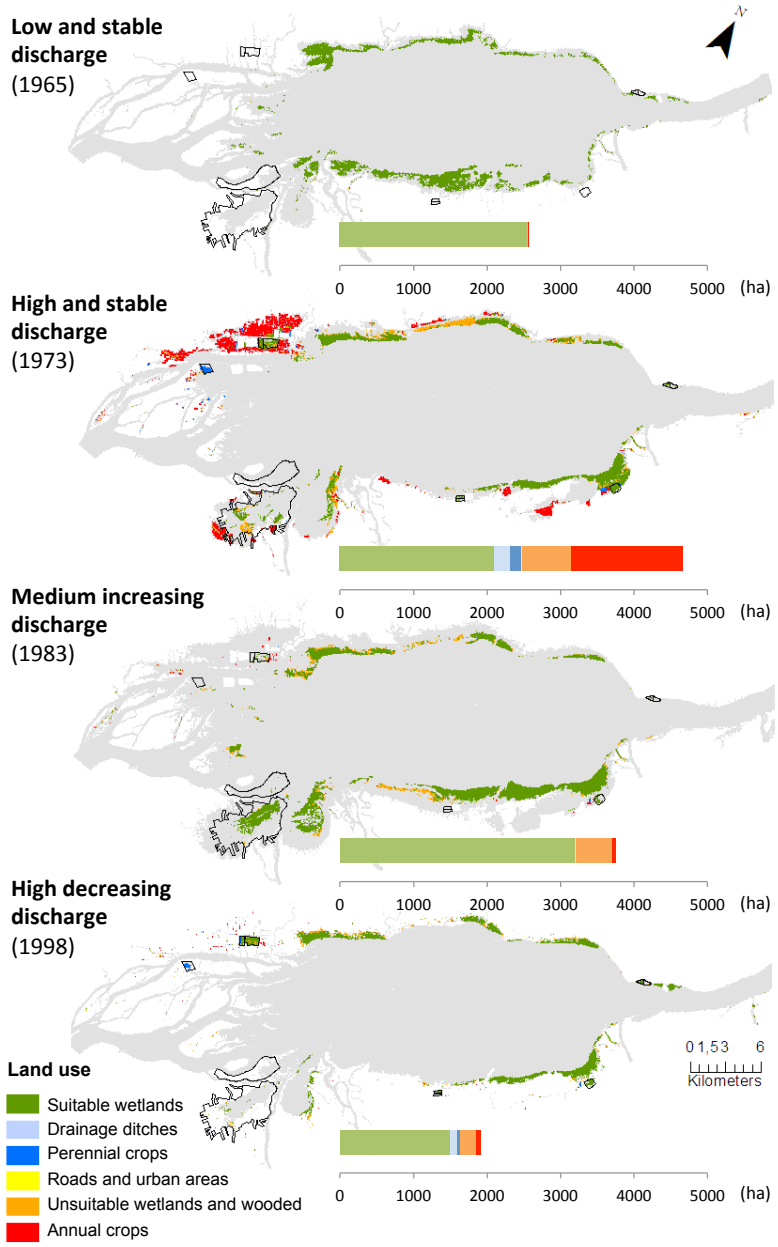

Figure 3.6 Connected spawning habitats were overlaid to the contemporary land-use of the Lake Saint-Pierre (2014' description) to identify effective (green and blue colors) and non-effective (yellow, orange and red colors) spawning habitats for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998).

When considering the contemporary land-use alterations on connected spawning habitats, water discharge increasing from medium to high water level between the maximum spawning time ($Week_0$) and the free-swimming stage ($Week_5$) proved the most favourable hydrological conditions for northern pike recruitment in the Lake Saint-Pierre (increasing profile 1983 in Figure 3.7). In this case, 3,218 ha, corresponding to 70% of the initial potential spawning area, are connected to nurseries areas and not altered by unsuitable land-use (= effective spawning habitats). During a stable-low profile (1965), almost all the potential spawning areas are effective for northern pike recruitment (i.e. 2,549 ha, 91% of potential habitats). Although 2,463 ha of connected spawning habitats remained effective during a stable-high profile (1973), corresponding to only 47% of the potential area. This important drop being caused by agricultural practices. During a decreasing profile (1998), potential habitats theoretically altered by the land-use were already lost to hydrological constrains on habitat connectivity. Although only 27% (1,628 ha) of potential spawning habitats remained effective in 1998, only 15% (279 ha) of connected spawning habitats were altered by the land-use. Finally, 332 ha of effective spawning habitats were spatially recurrent during the four contrasted hydrological profiles (dark green in Figure 3.7).

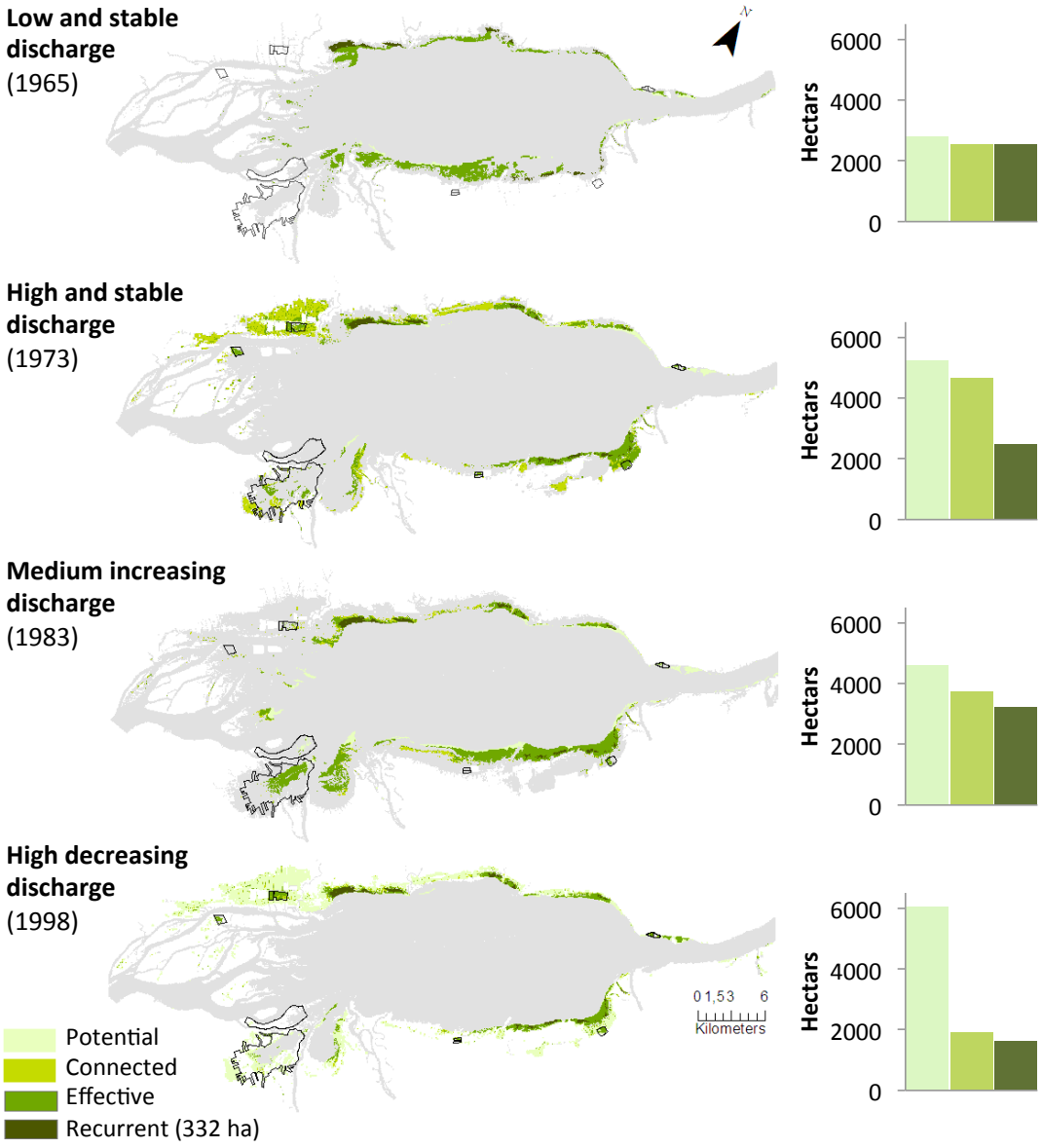

Figure 3.7 Spawning habitat area as (1) potential, (2) connected, (3) effective and (4) recurrent in the Lake Saint-Pierre floodplain (St. Lawrence River, Canada). Recurrent habitats correspond to effective spawning habitats localised at the same area independently of the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998).

3.5 Discussion

The comparison between unaltered landscapes to contemporary altered Lake Saint-Pierre proved an invaluable tool allowing the identification and the quantification of key anthropogenic pressures influencing recruitment of early-life history stages in a typical large-river floodplain. Our simulations demonstrated that both water discharge regulation and increasing intensive agriculture in the floodplain drastically reduced the effective spawning habitats of species exploiting the upper littoral portion of a river such as northern pike. Combined together, those two pressures led to a paradoxical situation. The years with low water discharges, usually corresponding to low fish reproduction potential, became in the present context the most productive within the time series since it retain it's full, albeit small, potential while the productivity potential of years with high water discharges is been culled by the direct spatial overlap between agriculture and spawning habitats.

3.5.1 Consequences of water discharge regulation on effective spawning habitats

Water discharge regulation has profoundly altered the natural hydrological regime and consequently reduced the effective spawning habitats in productive floodplains. The largest effective spawning habitat areas are observed during increasing profile, a hydrological condition less recurrent in the SLR since the implementation of water regulation. Although an increasing profile between the maximum spawning time ($Week_0$) and the beginning of the free-swimming stage ($Week_5$) was observed in 14% of the years analysed between 1965-2013 (Foubert *et al*. in prep, see chapter II in the present thesis), this situation was the most frequent before the Ottawa River became regulated in 1911 (Morin et Bouchard 2000). In contrast, the most recurrent hydrological condition since 1965 is a steadily decreasing profile between $Week_0$ and $Week_5$, a hydrological condition resulting in the smallest effective spawning habitat area in the Lake Saint-Pierre. Indeed, a rapid dewatering after pike eggs deposition turned out vast areas of spawning habitat in mortality traps. Moreover, decreasing

profile may transform moderately dense vegetation associated to high quality spawning and nursery habitats (Casselman et Lewis 1996; Timm et Pierce 2015) in very dense macrophyte beds with low oxygen levels (Casselman 1978; Holland et Huston 1984). As the Ottawa River is the major tributary of the SLR, with a water discharge ranging from 570 to 9,200 $m^3.s^{-1}$ (Carpentier 2003), its regulation has completely transformed the flooding profile during springtime, and hence is now limiting years generating large effective spawning area in the Lake Saint-Pierre floodplain.

In addition, annual maximum water discharge has drastically reduced in the SLR since Ottawa River regulation (i.e. nearly of 2,500 $m^3.s^{-1}$), a decrease exacerbated by the regulation of water levels in Lake Ontario in 1958 (i.e. reduction of 1,020 $m^3.s^{-1}$; Morin et Bouchard 2000). The reduction of maximal water discharges, observed during consecutive years, limited the surface area available for northern pike spawning and availability of large nursery areas, this situation is quite obvious in the Lake Saint-Pierre archipelago (Brodeur *et al*. 2006). Such conditions may contribute to the steady decline of riverine fish population in major river systems (e.g. Goto *et al*. 2015). Moreover, the water regulation of the SLR has shortened the duration of the flood by three weeks compared to the natural regime (Morin et Bouchard 2000). This increases the risk of habitat dewatering which reduce eggs and larvae survival for many riverine fish (Dumont et Fortin 1977).

3.5.2 Interactions between agricultural activities and hydrological variations

Stable-high water discharges that are naturally favourable to riverine fish recruitment in large floodplains (Junk *et al*. 1989; Gorski *et al*. 2011) have lost their productive habitats because of anthropogenic pressures. Although a stable-high profile in the Lake Saint-Pierre, illustrated by the simulation done for 1973, generated large area of spawning habitats connected to nurseries (4,665 ha), only 47% were effective to larval survival during the five first week of the pike's ontogeny because of agriculture

practices. Consequently, stable-high and stable-low profiles generate comparable surfaces of effective spawning habitats (2,463 ha in 1973 vs. 2,549 ha in 1965). The expansion of unsuitable land-use activities in the floodplain (i.e. unsuitable wetlands and wooded, the development of annual crops, roads and urban areas) altered 2 201 ha of theoretically connected spawning habitats (if the system was "unaltered" by human activities) where 1 517 ha of the total surface loss is lost only because of agricultural practices. In recent years, the Lake Saint-Pierre's natural habitats and perennial crops (i.e. pasture and forage crops) were progressively converted to annual crops (e.g. wheat, corn and soya, Martin et Létourneau 2011). While perennial crops can be used successfully as fish habitat, conversion of such production toward annual crops transforms these previously high-quality habitats in the worst areas to be use by fishes. As a consequence, in recent years the potential for stable-high profiles in generating strong cohorts that favoured the presence of large northern pike populations were systematically culled by human activities.

In agricultural landscapes, drained ditches and managed wetlands appear as key landscape features maintaining high-quality habitats and facilitating connectivity. Our results highlighted the role of both features in maintaining effective spawning habitats in the upper part of the floodplain, where land exploited by humans and other potentially flooded areas became vulnerable to dewatering (e.g. in 1998 and 1973 in the Maskinongé Bay). Even if managed wetlands are only accessible during medium to high water discharges (Brodeur *et al*. 2004), these landscaping favor the spatial overlap of spawning and nursery habitats which improve larval growth and survival (Schiemer *et al*. 2001; Ospina-Alvarez *et al*. 2012). Moreover, when spawning and nursery habitats are spatially disjoint, drained ditches network can be used by mobile individuals to connect nursery habitats (e.g. Ishiyama *et al*. 2014). Even if young pike larvae have low swimming capacities, low current speeds in large floodplains favor larval dispersal toward nurseries (Schiemer *et al*. 2003; Miehls et Dettmers 2011, Foubert *et al*. in prep see chapter II in the present thesis). Several independent

observations on the Lake Saint-Pierre confirm the presence of northern pike larvae in drained ditches and managed wetlands are considered as effective spawning habitats (unpublished data).

3.5.3 Implications for management

Restoration of natural habitats and connectivity are recognized as concrete management actions for dealing with fragmented landscapes (Beier et Noss 1998). Results of the study revealed key elements that should be taken in consideration for restoring Lake Saint-Pierre northern pike stocks. Namely, the conversion of large intensive agriculture to natural areas or perennial crops that are used successfully as fish habitat is required to improve the Lake Saint-Pierre ecosystem health (e.g. Washitani 2007; Gagliardi et Pettigrove 2013). Areas where large connected habitats are altered by agriculture, such as Maskinongé Bay, have to be targeted first (Figure 3.1, Figure 3.6). Moreover, the maintenance of drained ditches networks, which contributes to habitat connectivity in the floodplain, will improve early-life recruitment by favouring eggs and larval survival. Even if the road network can restrict connectivity in floodplains (Doyle *et al*. 2008; Blanton et Marcus 2014), flow-through structures such as culverts proved to be useful to maintain connectivity in large anthropised floodplains (Douven *et al*. 2012; Le Pichon *et al*. in prep). The effectiveness of managed wetlands, which prolong the flood duration, encourages the creation of new protected areas. As for Lake Ontario, searching for new regulatory rules for managing water levels of the Ottawa River could benefit species exploiting the floodplains of the SLR through the re-creation of more natural spring flood profile. The International Joint Commission (IJC), created by the Boundary Water Treaty Act of 1909 between United States and Canada, approve a new management plan in 2016 allowing more water levels variations of the Lake Ontario – SLR system. In comparison, the alterations induced by the Ottawa River regulation are far less known and little considered. However, the Ottawa River regulation drastically

changed the natural SLR flow regime generating impacts on aquatic fauna and their habitats.

To conclude, water regulation rules and agricultural practices profoundly reduced the natural productivity of a large floodplain by generating almost yearly low effective habitats, which do not allow sustaining stocks level to their past abundance. In a context of global climate change, where a reduction of spring water discharge and an increase of extreme hydrological conditions are expected (Mortsch *et al*. 2000; Boyer *et al*. 2010), surfaces of effective spawning habitats in the Lake Saint-Pierre may be further be reduced. This perspective stresses the need to restore production potential of years with high water discharges. Restoring habitat-quality and connectivity in floodplains will play an important role in conserving biodiversity and maintain sustainable populations.

3.6 Acknowledgments

This study would have been impossible without the contribution of the members of the Thousand Islands Biological Station to the field experiences and of Sylvain Martin to the hydrological data exports. A special thanks to Dr M. Cusson for these revisions of the manuscript. This study is part of A.F.'s Ph.D. thesis. Financial support was provided by grants from the "Chaire de Recherche sur les Espèces Aquatiques Exploitées" (CREAE), from the present Ministère de la Faune, des Forêts et des Parcs du Québec (MFFP), from the "Ressources Aquatiques Québec" (RAQ), and from the Commission permanente de coopération franco-québécoise (CPCFQ).

CONCLUSION GÉNÉRALE

La présente thèse a permis d'évaluer plusieurs caractéristiques du paysage de la portion fluviale du Saint-Laurent (Québec, Canada) pouvant expliquer les réponses des communautés de poissons et de certaines de leurs populations. Bien que des caractéristiques semi-permanentes du paysage telle que l'alternance de lacs fluviaux, de corridors et d'archipels, structurent les communautés de poissons, son caractère dynamique à plus fine échelle spatio-temporelle détermine la connectivité des habitats des jeunes stades de vie du grand brochet, une espèce indicatrice de la santé de la plaine d'inondation. L'application des concepts et méthodes de type « riverscape » a permis de mettre en évidence des patrons dans la structure des communautés de poissons à différentes échelles (gradient longitudinal, unités hydro-morphologiques, secteurs et rives) tout en soulignant la variabilité spatiotemporelle des habitats aquatiques. Ces caractéristiques élargissent le cadre d'analyse du fleuve Saint-Laurent en s'appuyant davantage sur une réalité écologique et, nous l'espérons, contribueront à améliorer la gestion des poissons d'eau douce et la protection ou la restauration de leurs habitats. Les outils développés dans la présente thèse pourraient être transférés à d'autres grands fleuves, à condition de calibrer et valider les modèles à leurs nouveaux contextes.

4.1 Processus écologiques à l'échelle du paysage

4.1.1 Niveau d'organisation : la communauté

4.1.1.1 Patrons longitudinaux de diversité

Le patron global de la diversité des poissons d'eau douce le long du fleuve Saint-Laurent (≈ 400 km) reflète la grande hétérogénéité du paysage et la particularité de chacun des secteurs aux caractéristiques hydro-morphologiques distinctes (≈ 15-

50 km). Par exemple, la zone de transition entre la portion fluviale et l'estuaire moyen, représentée par les secteurs de Bécancour-Batiscan et Grondines-Saint-Nicolas (=estuaire fluvial, Figure 0.3), abrite une communauté de poissons particulièrement diversifiée qui n'avait jusqu'à présent jamais été mise en évidence. De par sa position géographique le long du continuum, des espèces fluviales et estuariennes ont été capturées dans le secteur Grondines-Saint-Nicolas (par ex. poulamon atlantique, esturgeon noir, bar rayé). Ces deux secteurs, qui s'étalent sur près de 100 km, sont étroits, sinueux et influencés par une marée d'eau douce dont le marnage de l'ordre de 30 cm à Bécancour augmente progressivement vers l'aval et peut atteindre six mètres à Québec (Centre-Saint-Laurent 1996; Gauthier 2000). En plus de ces caractéristiques hydro-morphologiques uniques, le paysage aquatique de l'estuaire fluvial a été moins affecté par les activités humaines que certains secteurs en amont. Alors que la régularisation des débits en amont a profondement modifié les habitats du lac Saint-François, ces effets diminuent progressivement vers l'aval avec l'apport des tributaires et disparaissent avec le signal de la marée dans l'estuaire fluvial.

4.1.1.2 Différences entre les rives

Les contrastes de diversité entre les rives sont rarement considérés dans les systèmes fluviaux. Dans le fleuve Saint-Laurent, les rives opposées abritent des communautés de poissons différentes, autant dans des lacs fluviaux très larges (largeur de 11-13 km aux lacs Saint-Louis et Saint-Pierre) que dans des secteurs plus étroits (largeur de 3 km dans le secteur Bécancour-Batiscan). Les caractéristiques et modifications du paysage aquatique telles que l'hétérogénéité des habitats, la distance entre les rives separées par un profond chenal de navigation, ainsi que la présence de différentes masses d'eau peuvent expliquer les diverses réponses observées le long de ce grand fleuve. De manière surprenante, il arrive que des communautés de poissons de secteurs adjacents mais aux caractéristiques hydro-morphologiques distinctes (telles que la rive nord du lac Saint-Pierre et du corridor Bécancour-Batiscan) ne se

différencient pas systématiquement. Cela pourrait suggérer une plus grande connectivité entre les communautés de ces deux secteurs grâce à la possibilité et la capacité de dispersion des espèces. Bien que cela n'enlève en rien la robustesse du portrait obtenu, des analyses supplémentaires permettraient de déterminer le rôle de la dispersion des espèces et des différentes mosaïques d'habitats dans la structure de ces communautés (par ex. Erős *et al*. 2017).

4.1.2 Niveau d'organisation : la population

4.1.2.1 Particularités des lacs fluviaux

Lorsqu'on s'intéresse au rôle de la connectivité à plus fine échelle spatio-temporelle, les processus spatiaux qui agissent dans les plaines inondables du lac Saint-Pierre se distinguent de ceux observés dans le corridor Montréal-Sorel (chapitre II). Ces différences pourraient en partie expliquer les dissimilarités que l'on observe au niveau des communautés de poissons de ces deux secteurs distincts (chapitre I). En effet, alors que les habitats de reproduction sont peu abondants dans le corridor Montréal-Sorel et sujets à de forts courants (>10 $cm.s^{-1}$), le lac Saint-Pierre présente quant à lui une vaste étendue de frayères et de nourriceries propices aux poissons littoraux comme le grand brochet. Néanmoins, les fluctuations du régime hydrologique (c.-à-d. le marnage, la durée et la périodicité du niveau de l'eau) jouent un rôle majeur dans le lac fluvial et génèrent des habitats dont la surface, le patron spatial, et la connectivité sont très variables dans le temps. Par exemple, alors qu'une diminution rapide du niveau de l'eau assèche la majorité des habitats potentiels du lac Saint-Pierre (= trappes écologiques), une augmentation du niveau de l'eau génère de grandes superficies de frayères effectives (= connectées aux nourriceries). De plus, il arrive que des frayères soient connectées à des nourriceries plus distantes grâce aux faibles courants (< 10 $cm.s^{-1}$) qui favorisent le transport passif des larves dans la plaine d'inondation (Schiemer *et al*. 2003; Miehls et Dettmers 2011). Ce mécanisme de dispersion, évalué au lac Saint-Pierre dans le chapitre II, permet de potentiellement

connecter des nourriceries à des frayères séparées par une distance atteignant jusqu'à 3 km. À titre de comparaison, cette distance est 5 fois supérieure aux observations faites dans des lacs intérieurs qui ne sont pas parcourus par des courants aussi élevés (Cucherousset *et al*. 2009; Skov *et al*. 2011). Cela dit, la superposition des frayères et des nourriceries, qui est largement favorisée par la stabilité des conditions hydrologiques dans le lac Saint-Pierre, pourrait davantage assurer le succès de reproduction des espèces qui exploitent le haut des plaines inondables (faible risque de mortalité et faibles couts énergétiques, Schiemer *et al*. 2001).

4.1.2.2 Importance de la connectivité entre les frayères et les nourriceries

Lorsqu'on considère la connectivité entre les zones de fraie et de nourricerie, certaines frayères ayant un fort potentiel pour les géniteurs peuvent devenir de réelles trappes écologiques pour les œufs et les larves (Jeffres et Moyle 2012; Hufnagl *et al*. 2013; Sheaves *et al*. 2014). Dans le lac Saint-Pierre et le corridor Montréal-Sorel, toutes les frayères potentielles ne contribuent pas au succès de reproduction du grand brochet. Il faut donc faire une distinction entre « frayères potentielles », s'adressant à tous les habitats adéquat pour le dépôt des œufs (Mingelbier *et al*. 2008a), et « frayères effectives » correspondant aux frayères connectées avec les nourriceries, répondant à des besoins plus étendus dans le cycle de vie en partant de l'oeuf jusqu'au stade larve libre. Dans le cas du grand brochet, les œufs et les larves se développent attachés à la végétation des frayères pendant près de quatre semaines (Fortin *et al*. 1982; Massé *et al*. 1988; Vallières et Fortin 1988), ce qui les rend particulièrement sensibles aux variations de niveau d'eau durant cette période. Bien que le grand brochet soit adapté à la variabilité des conditions environnementales en éparpillant ses œufs dans différents sites de fraie (Vallières et Fortin 1988; Ouellet-Cauchon *et al*. 2014), la régularisation du débit du fleuve Saint-Laurent et de ses tributaires ainsi que l'expansion de l'agriculture jusque dans la plaine d'inondation ont réduit et fragmenté ses habitats de fraie et de nourricerie. Ces deux usages humains et les effets qui en découlent sur le grand brochet peuvent en partie expliquer

le déclin de l'abondance de cette espèce qui s'observe depuis les années 1990 dans le fleuve Saint-Laurent (Smith *et al*. 2007; Vachon *et al*. 2014). Sachant que les habitats utilisés par le grand brochet lors des premiers stades de vie sont succeptibles d'être utilisés par d'autres espèces littorales, les modifications observées ont pu affecter l'ensemble de la communauté de poissons qui utilise la plaine inondable du lac Saint-Pierre. D'ailleurs, la faible valeur de diversité observée au lac Saint-Pierre (chapitre I) témoigne de la dégradation et de la fragmentation de son paysage aquatique.

4.2 Contributions à la gestion de la ressource ichtyologique

4.2.1 Biodiversité

Protéger les « points chauds » de biodiversité est l'un des objectifs principaux dans le domaine de la conservation. Or, la biodiversité est un concept complexe qui a de multiples facettes (Magurran et McGill 2011). Il n'existe pas une diversité unique. Au même titre qu'il n'existe pas une façon unique de mesurer la biodiversité (par ex. Maire *et al*. 2013). Dans le fleuve Saint-Laurent, les études ayant mesuré les variations de diversité des communautés de poissons s'appuyaient principalement sur le nombre d'espèces ou sur un indice d'intégrité biotique composé d'une dizaine de descripteurs (La Violette *et al*. 2003; mise à jour dans Mingelbier *et al*. 2008b). Alors que le nombre d'espèces est fortement biaisé par l'effort d'échantillonnage (Gotelli et Colwell 2001), l'interprétation de l'indice d'intégrité biotique est difficile dans le fleuve Saint-Laurent (Mingelbier *et al*. 2008b). Dans le chapitre I de la présente thèse, la distinction de plusieurs aspects de la diversité (raréfaction, spécifique, taxonomique) permet d'identifier des « points chauds » de biodiversité robustes et complémentaires. Le long du fleuve Saint-Laurent, la mosaïque d'habitats de l'Archipel du lac Saint-Pierre, reconnu depuis les années 2000 par l'UNESCO comme réserve de la Biosphère, abrite la communauté de poissons dont la valeur de diversité spécifique est la plus élevée. En parallèle, le secteur Grondines-Saint-Nicolas, peu documenté et plus rarement considéré dans les mesures de gestion,

présente la plus forte valeur de diversité taxonomique et abrite une communauté de poissons très différente des autres secteurs. Ces résultats témoignent de l'intérêt d'un échantillonnage standardisé à large échelle qui maintiendrait l'estuaire fluvial dans la zone d'étude (c.-à-d. Bécancour-Batiscan et Grondines-Saint-Nicolas). De plus, la difficulté de synthétiser les multiples facettes de la diversité dans un indice unique montre l'utilité de mesurer séparément plusieurs indices dont les réponses sont complémentaires.

4.2.2 Connectivité

Au même titre que la biodiversité, la conservation et la restauration de la connectivité des habitats, qui favorisent la diversité et la productivité d'un écosystème, sont devenues d'importants leitmotivs en sciences de la conservation. À l'échelle du fleuve, la quasi totalité de la portion fluviale du Saint-Laurent, entre le lac Saint-Louis et l'estuaire fluviale, est connectée. Cette caractéristique, qui favorise la diversité ichtyologique de ce grand fleuve et la dispersion des espèces, doit être conservée. Bien que les effets des barrages de Cornwall et Beauharnois sur la rupture de connectivité longitudinale et la faible valeur de diversité du lac Saint-François soient documentés (La Violette *et al*. 2003), la dissimilarité des communautés de poissons des rives opposées suggère un manque de connectivité transversale dans le fleuve Saint-Laurent. Certaines modifications du paysage, telle que la présence d'un large et profond chenal de navigation, pourraient expliquer ce phénomène. Ce résultat permet de complèter le portrait sur l'effet des modifications anthropiques sur les communautés de poissons et donne des pistes de reflexions pour les futures études et actions.

À plus fine échelle spatio-temporelle, les résultats de la présente thèse soulignent plusieurs facettes de la connectivité à considérer afin d'identifier des « frayères effectives » et d'éviter de créer des aménagements inadéquats conduisant à la création de trappes écologiques. En premier lieu, la connectivité des habitats peut changer

rapidement dans le temps en fonction des conditions hydrologiques (par ex. lors de la crue printanière, Junk *et al*. 1989). La modélisation des habitats devient alors un outil utile à la gestion afin d'identifier les frayères effectives et récurrentes induites par des conditions hydrologiques contrastées (localisation sur la Figure 3.7 du chapitre III). En second lieu, les variables environnementales qui limitent ou facilitent la connectivité ne sont pas les mêmes dans un corridor étroit que dans un lac fluvial en raison de leur caractéristiques hydro-morphologiques distinctes. Par exemple, alors que la forte vitesse du courant (> 10 $cm.s^{-1}$) domine dans le corridor Montréal-Sorel et restreint la connectivité entre les frayères et les nourriceries, la diminution du niveau de l'eau peut, quant à elle, assécher de vastes surfaces d'habitats dans le lac Saint-Pierre. Enfin, certains éléments anthropiques qui façonnent le paysage des plaines d'inondation peuvent faciliter ou limiter la connectivité (par ex. Washitani 2007; Blanton et Marcus 2014). Alors que la présence de marais aménagés, de drains agricoles et de ponceaux maintient un réseau d'habitats connectés au lac Saint-Pierre, l'agriculture intensive, les infrastructures de transport et la régularisation des débits du fleuve Saint-Laurent et de ses tributaires sont des éléments limitants la connectivité des habitats.

4.2.3 Unités écologiques de gestion à différentes échelles spatiales

Les plans de conservation et de restauration des milieux naturels s'appuient sur des unités géographiques reflétant une réalité écologique à différentes échelles spatiales. Les résultats de cette thèse permettent d'affiner ces unités de gestion grâce à une meilleure compréhension des processus écologiques qui gouvernent les communautés de poissons et certaines de leurs populations du fleuve Saint-Laurent.

À l'échelle des habitats effectifs (dans cette étude < 3 km), les frayères à conserver ou à restaurer doivent être connectées à une nourricerie afin d'assurer un meilleur succès de reproduction. Le chapitre III de cette thèse identifie les frayères effectives à conserver ou à restaurer dans le lac Saint-Pierre (Figure 4.1). Concrètement, les

frayères qui sont à la fois connectées lors de conditions hydrologiques contrastées et non altérées par l'utilisation du sol (= 332 ha) sont à conserver (en vert). Par ailleurs, d'autres frayères effectives lors d'évènements potentiellement productifs pour le grand brochet (c.-à-d. niveau d'eau haut et stable) et perdues à cause de l'utilisation du sol sont à restaurer (en rouge et orange). Cela correspond à 2 201 ha dont 1 517 ha sont altérés par l'agriculture intensive. Les frayères effectives identifiées dans la Figure 4.1 se distinguent en fonction du processus spatial qui les connecte à une nourricerie, c'est-à-dire par chevauchement ou par dispersion. Les frayères effectives par chevauchement sont à conserver et à restaurer en priorité car elles favorisent la survie et la croissance des larves. En ce qui concerne les frayères effectives par dispersion, les résultats du chapitre II et III suggèrent d'étendre les zones protégées à un rayon minimum de 600 m au lac Saint-Pierre et de 150 m dans le secteur Montréal-Sorel afin d'optimiser la dispersion des larves vers les nourriceries (voir les analyses réalisées sur le coefficient de dispersion α : Figure 2.8 du chapitre II et appendice Figure C.2 du chapitre III). Le cas de la baie Maskinongé (nord-ouest du lac Saint-Pierre) met en évidence le rôle clé joué par les marais aménagés et les drains agricoles, en cela qu'ils procurent des frayères effectives et non altérées par l'utilisation du sol (bleu clair sur la Figure 4.1). La superficie des marais aménagés, qui prolongent la durée de la crue dans la plaine inondable du lac Saint-Pierre, pourrait être étendue. Par exemple, certains marais aménagés pour la sauvagine (en pointillés) pourraient assurer une double vocation de protection de la sauvagine et des poissons. Enfin, l'importance des drains agricoles et des ponceaux dans la connectivité des habitats souligne l'importance qu'ils soient correctement entretenus afin de les garder fonctionnels.

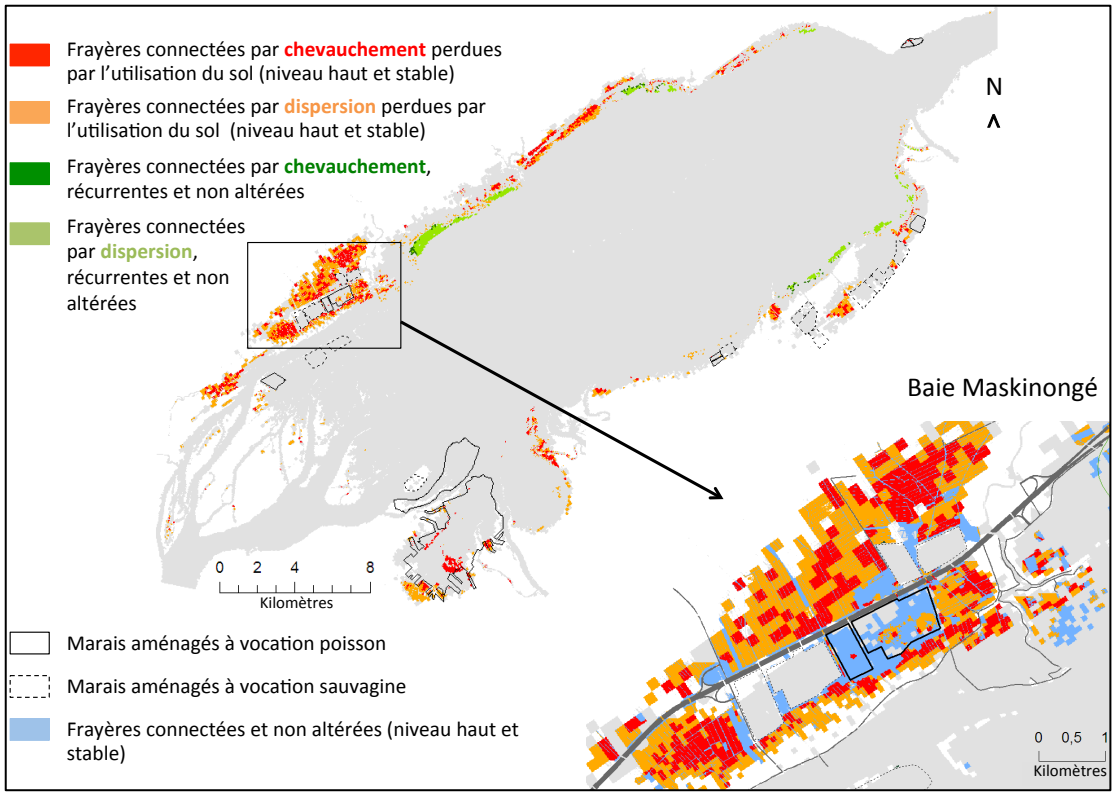

Figure 4.1 Conservation et restauration des habitats des jeunes stades de vie du grand brochet dans la plaine inondable du lac Saint-Pierre (fleuve Saint-Laurent, Canada).

À plus large échelle spatiale (15-50 km), les secteurs reflètent les grandes discontinuités hydro-morphologiques le long du fleuve Saint-Laurent structurant les communautés de poissons (chapitre I). De plus, les processus spatiaux observés à plus fine échelle qui limitent ou facilitent la connectivité des habitats ne sont pas les mêmes dans un corridor étroit que dans un lac fluvial (chapitre II). Cette échelle de gestion est donc pertinente, surtout pour les secteurs où l'on n'observe pas de différences entre les communautés des rives opposées : lac Saint-François, Montréal-Sorel et Grondines-Saint-Nicolas. Pour les autres secteurs, c'est-à-dire le lac Saint-Louis, l'archipel de Sorel, le lac Saint-Pierre et le corridor Bécancour-Batiscan, les rives présentent des communautés de poissons structurées différemment et qui

pourraient nécessiter d'être prises en compte par la gestion. Par exemple, l'effet des pressions anthropiques telles que l'urbanisation et l'agriculture peuvent différer d'une rive à l'autre et forcer les gestionnaires à travailler avec des acteurs distincts. De plus, les différences dans la structure des communautés de poissons de rives opposées peuvent amener à les considérer dans des unités de gestion séparés. Aussi, certaines mesures pourraient être plus sévères sur une rive si l'abondance de l'espèce visée est plus faible que sur l'autre rive. Bien que cet exemple soit simplifié et mériterait d'être bien documenté (par ex. dynamique source/puit), il vise à montrer l'importance de considérer l'échelle de la rive dans la gestion de certains secteurs du Saint-Laurent.

À l'échelle du fleuve Saint-Laurent, le continuum amont-aval force à adopter une approche globale de conservation et de restauration au moins à l'échelle de la portion fluviale du Saint-Laurent. Par exemple, le régime hydrologique du fleuve Saint-Laurent, qui a été fortement modifié dès 1911 suite à la construction des premiers grands barrages sur la rivière des Outaouais (principal tributaire) et, ensuite, durant les années 1930-1960 par de nombreux travaux de régularisation sur le système lac Ontario-Saint-Laurent, a encore aujourd'hui des effets sur l'ensemble du tronçon fluvial du Saint-Laurent (par ex. Brodeur *et al*. 2006). Ces nombreuses interventions physiques ont notamment réduit la diversité de la communauté de poissons du lac Saint-François (chapitre I) et ont réduit la superficie d'habitats effectifs du lac Saint-Pierre (chapitre III). Alors qu'un nouveau plan de régularisation du débit sortant du lac Ontario a pris effet en 2016 afin de retrouver un signal plus naturel, aucune initiative n'a encore été entreprise dans ce sens concernant la régularisation du débit de la rivière des Outaouais, dont les effets sont jusqu'à dix fois plus élevés que ceux de la régularisation du système lac Ontario-Saint-Laurent. En effet, à titre comparatif, avant la régularisation de l'Outaouais, les crues à Sorel duraient approximativement trois semaines de plus et le niveau d'eau au Lac Saint-Pierre était en moyenne 0,75 m plus élevé qu'aujourd'hui (Morin et Bouchard 2000). Il y aurait aujourd'hui certainement des possibilités d'adapter la régularisation du débit de la rivière des

Outaouais en vue de restaurer dans le fleuve Saint-Laurent une partie du potentiel des habitats des poissons et de leur connectivité. Une option consisterait à prolonger la crue dans les milieux déjà inondés afin d'assurer un chevauchement entre les frayères et les nourriceries. Cette option mériterait d'être examinée plus en détail.

4.3 Perspectives de recherche et améliorations possibles

Bien que les analyses réalisées lors de ma thèse aient été menées avec rigueur et que les résultats obtenus soient à mon sens pertinents, chaque chapitre ouvre de nouvelles perspectives de recherche et des pistes d'amélioration dont voici quelques exemples.

4.3.1 Organisation des communautés de poissons

Le portrait de la diversité des communautés de poissons du chapitre I, qui s'appuie sur des analyses robustes le long de la portion fluviale du Saint-Laurent, pourrait être complété par (1) la précision du lien entre l'organisation des communautés et les caractéristiques du paysage, (2) la mesure d'autres aspects de la diversité, (3) en tenant compte d'un plus vaste territoire et (4) d'observations historiques. En effet, le lien entre l'organisation spatiale des communautés de poissons et les caractéristiques du paysage aquatique pourrait être précisé grâce à la mesure de métriques reliées à l'hétérogénéité et à la connectivité des habitats. Par exemple, des indices mesurant la diversité peuvent être utilisés avec des variables d'habitats, telles que la composition et/ou la structure de la végétation, afin de mesurer le degré d'hétérogénéité de chaque segment. Ce résultat pourrait être comparé à la valeur de diversité de chaque communauté de poissons afin d'évaluer leur corrélation.

Concernant la diversité, les aspects spécifique et taxonomique pourraient être avantageusement complétés par une analyse approfondie des fonctions de l'écosystème (Magurran et McGill 2011). Des analyses préliminaires de la diversité fonctionnelle indiquent que lorsque l'on regroupe les espèces de poissons du fleuve Saint-Laurent en fonction de leur taille, leur alimentation, leur préférence d'habitats,

et leur potentiel de migration, les patrons obtenus sont similaires à la diversité spécifique. Bien que ce résultat puisse suggérer que la diversité spécifique reflète les fonctions de l'écosystème, ces analyses mériteraient d'être approfondies pour en tirer de plus robustes conclusions. En effet, les critères utilisés pour regrouper les espèces sont peu discriminants dans le fleuve Saint-Laurent car plusieurs groupes ne contiennent qu'une seule espèce. De plus, une revue de littérature sur les nombreux indices fonctionnels récemment développés permettrait d'en faire un choix plus éclairé.

Pour compléter le portrait de la diversité des communautés de poissons et souligner d'autres processus impliqués dans la diversité et la productivité du fleuve, il serait bénéfique d'étendre la zone d'étude à la portion internationale du fleuve Saint-Laurent en amont du barrage Moses-Saunders qui fait l'objet de suivis réguliers, à son estuaire en aval (Réseau d'Inventaire des Poissons de l'Estuaire), à ses tributaires (échantillonnage du Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques) ou encore à d'autres habitats plus difficiles d'accès comme le chenal de navigation ou la Voie maritime (de la Chenelière *et al*. 2015).

Au-delà de l'aspect spatial sur lequel se concentre cette thèse, la variabilité des communautés de poissons dans le temps pourrait être évaluée grâce à l'utilisation d'un échantillonnage historique réalisé par J.R. Mongeau entre 1965 et 1974. À titre préliminaire et afin de s'assurer que ces données historiques et celles du Réseau de suivi ichtyologique (1995-2013) soient bien comparables, l'efficacité des engins utilisés a été testée au printemps 2013 dans l'archipel du lac Saint-Pierre. La composition et la structure des communautés de poissons capturés par les deux types d'engins étant comparables, il serait envisageable d'utiliser ces échantillonnages afin d'évaluer les changements survenus dans les communautés du fleuve depuis les

années 1960. Des analyses préliminaires montrent notamment une homogénéisation des communautés de l'archipel du lac Saint-Pierre entre 1971 et 2010 (Foubert 2011).

4.3.2 Connectivité des habitats des jeunes stades de vie

Les mesures de connectivité réalisées durant ma thèse reposent sur des simulations obtenues à partir de modèles d'habitats. Les modèles étant des simplifications du système réel, les futurs efforts de recherche devraient se concentrer sur la validation de la localisation des frayères effectives et du rôle de la dispersion des larves libres. Bien que nous soyons confiant à propos de la localisation des frayères altérées et non productives au lac Saint-Pierre (chapitre III), l'incertitude est plus élevée quant à la localisation des frayères effectives qui contribueront au recrutement. Au dela de vérifications sur le terrain difficiles à obtenir au stade larvaire, l'intégration de données empiriques sur le déplacement des larves entre les frayères et les nourriceries améliorerait l'estimation de la distance parcourue par les larves (paramètre α) qui joue un rôle clé. Étant donné que les déplacements en milieu naturel ouvert sont difficiles à observer (par ex. Foubert 2014 lors d'un échantillonnage au printemps 2014), il serait sûrement approprié de réaliser des expériences en laboratoire ou bien dans des milieux naturels confinés et contrôlés tels que des marais aménagés.

De plus, au regard du rôle important de la variabilité hydrologique sur la connectivité des habitats, il serait intéressant d'ajouter l'analyse d'un profil hydrologique « moyen » correspondant au profil le plus fréquent (c.-à-d. faible diminution du débit entre la période de fraie et de nourricerie, chapitre II). En effet, même si les quatre profils hydrologiques comparent des situations extrêmes et fournissent des tendances, l'analyse de ce profil moeyn permettrait de localiser les frayères effectives les plus fréquentes. Avec un outil plus adaptés qu'Anaqualand, il serait encore plus précis de modéliser les frayères effectives pour chaque année de la période 1965-2013 afin d'obtenir une carte représentant la fréquence des frayères effectives (et non uniquement des frayères et nourriceries potentielles, chapitre III). Celle-ci pourrait

ensuite être superposée avec une représentation actuelle de l'utilisation du sol afin de cibler les frayères effectives les plus fréquemment perdues par l'agriculture et à restaurer en priorité. Pour cela, les algorithmes développés dans *Anaqualand 2.0* pourraient être intégrés directement aux modèles 2D hydrodynamiques d'Environnement Canada (Morin et Bouchard 2000; Morin *et al*. 2005) afin d'augmenter considérablement la capacité des calculs.

Alors que les chapitres II et III de cette thèse identifient les frayères effectives, des analyses de connectivité complémentaires permettraient d'identifier les nourriceries effectives et les corridors de connectivité entre ces deux types d'habitats. Des analyses de ce type ont été réalisées au lac Saint-Pierre afin de mesurer l'effet du réseau routier sur la connectivité entre les frayères et les nourriceries du grand brochet. Celles-ci révèlent que les nourriceries sont plus sensibles aux variations hydrologiques que les frayères et identifient des corridors à protéger ou à restaurer (Le Pichon *et al*. in prep). Des analyses comparables pourraient être réalisées en tenant compte de la pression agricole qui joue un rôle majeur dans la plaine inondable du lac Saint-Pierre.

4.3.3 Nouvelles pressions

Alors que la présente étude se concentre principalement sur les effet de la régularisation du débit et de l'agriculture, d'autres pressions influencent l'organisation des communautés de poissons et leurs habitats (par ex. Foubert 2015; Mingelbier *et al*. 2016). Deux d'entre elles risquent notamment de changer le patron de biodiversité et d'accentuer les pertes d'habitats productifs le long du fleuve Saint-Laurent. Tout d'abord, la présence de la carpe de roseau (*Ctenopharyngodon idella*) dans le système Saint-Laurent a été confirmée au début de 2017 par le Ministère des Forêts, de la Faune et des Parcs du Québec. L'introduction de cette carpe asiatique envahissante est une réelle menace pour cet écosystème en raison de sa capacité à altérer de façon importante les herbiers aquatiques, ce qui peut entrainer une perte

majeure de biodiversité. Les conséquences de l'introduction de carpes asiatiques s'observent dans la rivière Illinois (bassin du Mississippi) où ces espèces ont entrainé des changements importants dans la structure des communautés de poissons (Solomon *et al*. 2016). Ainsi, le portrait de la diversité des poissons d'eau douce présenté dans le chapitre I pourrait constituer, en quelque sorte, un état de référence correspondant à une période précédant l'établissement d'une des espèces de carpes asiatiques dans le fleuve Saint-Laurent et pourrait être utilisé dans le futur pour des fins de comparaison.

Deuxièmement, sachant que les conditions hydrologiques exercent un effet important sur les habitats et la connectivité des plaines inondables du fleuve Saint-Laurent (chapitres II et III), il est logique de penser que les changements climatiques en influenceront la disponibilité. À ce titre, les projections hydrologiques futures des tributaires du fleuve Saint-Laurent prédisent une augmentation entre 50 et 200% du débit moyen du fleuve en hiver et une diminution de 40% au printemps (Boyer *et al*. 2010). L'augmentation de la température moyenne et la diminution du rapport neige/précipitation expliqueraient principalement ces tendances (Mortsch *et al*. 2000). Alors que l'augmentation du débit d'eau en hiver risque d'éroder le lit et les berges du fleuve et de réduire la survie des graines et des plantes qui façonnent les herbiers aquatiques du littoral, la diminution du débit au printemps risque de réduire l'étendue inondée, notamment au lac Saint-Pierre. Ces changements pourraient donc réduire davantage la superficie de frayères effectives au printemps. De plus, avec des extrêmes climatiques plus fréquents (Mortsch *et al*. 2000), on peut aussi s'attendre à observer occasionnellement des niveaux d'eau très élevés ayant le potentiel de produire de fortes cohortes de grand brochet dans la mesure où la végétation inondée est propice. Dans un contexte de plus en plus variable, ces évènements seront d'autant plus importants pour maintenir les populations de poissons. Cela dit, il faudrait disposer de plus d'informations sur la variabilité du climat pour en estimer plus justement les effets. Enfin, Boyer *et al*. (2010) prédisent une avancée de la crue

printanière du fleuve Saint-Laurent de 22 à 34 jours. Il pourrait en résulter divers effets antagonistes tels qu'un allongement bénéfique de la saison de croissance ou une perturbation de la reproduction du grand brochet suite à une exposition à des températures plus variables ou encore à une perte de synchronisme entre l'éclosion des larves et la production de nourriture (par ex. match-mismatch, Cushing 1990).

Dans un contexte de changements climatiques et de pressions qui continuent de s'accumuler sur les ressources ichtyologiques du fleuve Saint-Laurent, les gestionnaires sont amenés à prioriser des actions de conservation et de restauration. En plus des composantes écologiques considérées dans la présente étude, ils devront aussi appuyer leurs décisions sur des critères socio-économiques, ainsi que sur les besoins d'autres usagés. Cela souligne l'intérêt de former des équipes multidisciplinaires composées de chercheurs et de gestionnaires de divers horizons afin d'intégrer les connaissances scientifiques dans la gestion de problématiques environnementales d'envergure. Ayant réalisé ma thèse au cœur et en accord avec les mandats de la Direction de l'expertise sur la faune aquatique du Ministère des Forêts, de la Faune et des Parcs du Québec, j'ai l'espoir que mes résultats de celle-ci contribueront à améliorer la gestion des poissons d'eau douce du fleuve Saint-Laurent.

4.3.4 Transfert méthodologique à d'autres grands fleuves et à d'autres espèces

En terminant, je crois que certaines méthodes, analyses ou approches développées dans la présente thèse sont exportables à d'autres grands fleuves que le Saint-Laurent et même à d'autres espèces que le grand brochet. Voici deux exemples qui me paraissent être des éléments clés pour les futures recherches et pour la gestion de la ressource ichtyologique.

De part la taille unique des grands fleuves (c.-à-d. bassin versant > 900 000 km^2 et débit annuel > 7 500 $m^3 \cdot s^{-1}$, (Bethemont 2003), l'échelle de la rive pourrait devenir

une unité de gestion écologique appropriée. En effet, chacune des rives est succeptible d'abriter des communautés de poissons structurées différemment et reflètant diverses caractéristiques hydro-morphologiques et/ou modifications anthropiques du paysage. Cette échelle d'analyse pourrait s'avérer pertinent dans d'autres grands fleuves et procurerait une meilleure compréhension et une gestion plus adaptée de la ressource ichtyologique.

À plus fine échelle spatio-temporelle, la notion de « frayères effectives », qui souligne l'importance de considérer la connectivité entre les habitats assurant la complétion d'une importante étape du cycle de vie d'une espèce, pourrait être adaptée à d'autres espèces ou à d'autres habitats vitaux. Pour ce faire, il serait nécessaire d'adapter chaque étape de la modélisation aux besoins spécifiques de l'espèce et au contexte topographique et hydrologique. Par exemple, alors que le grand brochet est attaché à la végétation pendant quatre semaines, la perchaude devient mobile beaucoup plus rapidement et effectue des déplacements pélagiques. Cette spécificité pourrait potentiellement modifier la localisation des frayères effectives de ces deux espèces littorales.

Sachant que ces exemples de transfert méthodologiques ne sont pas exhaustifs, j'espère que la lecture de cette thèse saura inspirer et éclairer les chercheurs et les gestionnaires ayant pour responsabilités de protéger ou de restaurer les ressources ichtyologiques présentes dans les grands systèmes fluviaux.

APPENDICE A

CHAPITRE I

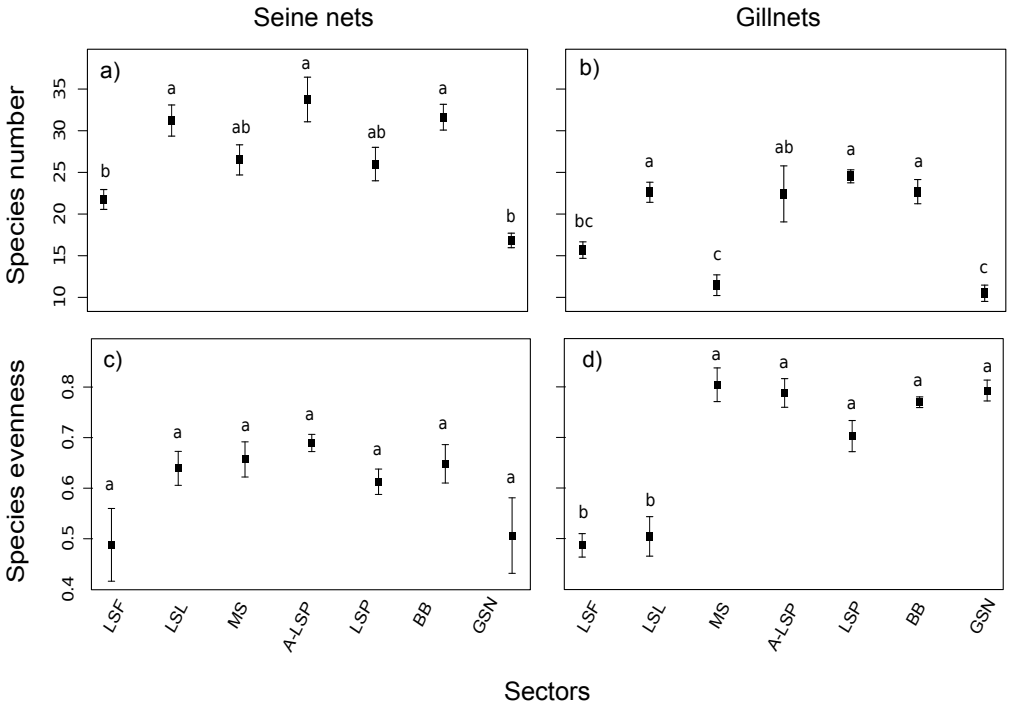

Figure A.1 Point bars showing the average (± SE) of species richness (S) and species evenness (J') among sectors (upstream to downstream) of the St. Lawrence River for seine net (graphs a, c) and gillnet (graphs b, d) samples. Different letters above bars represent significant differences (P <0.05, Holm adjustement).

Except for fish communities captured by both gears in 4-A-LSP (average of richness for seine nets: 38 versus 26, and gillnets: 27 vs 13, north and south respectively) and by gillnets in LSL (24 vs 19 north and south respectively), no difference was observed between north and south shores (detailed average per sectors/shores not shown). These indices reveal a high variability of fish communities captured by both gears along the river. However, even if they are simple and informative, there are largely biased by the gears used and sampling effort.

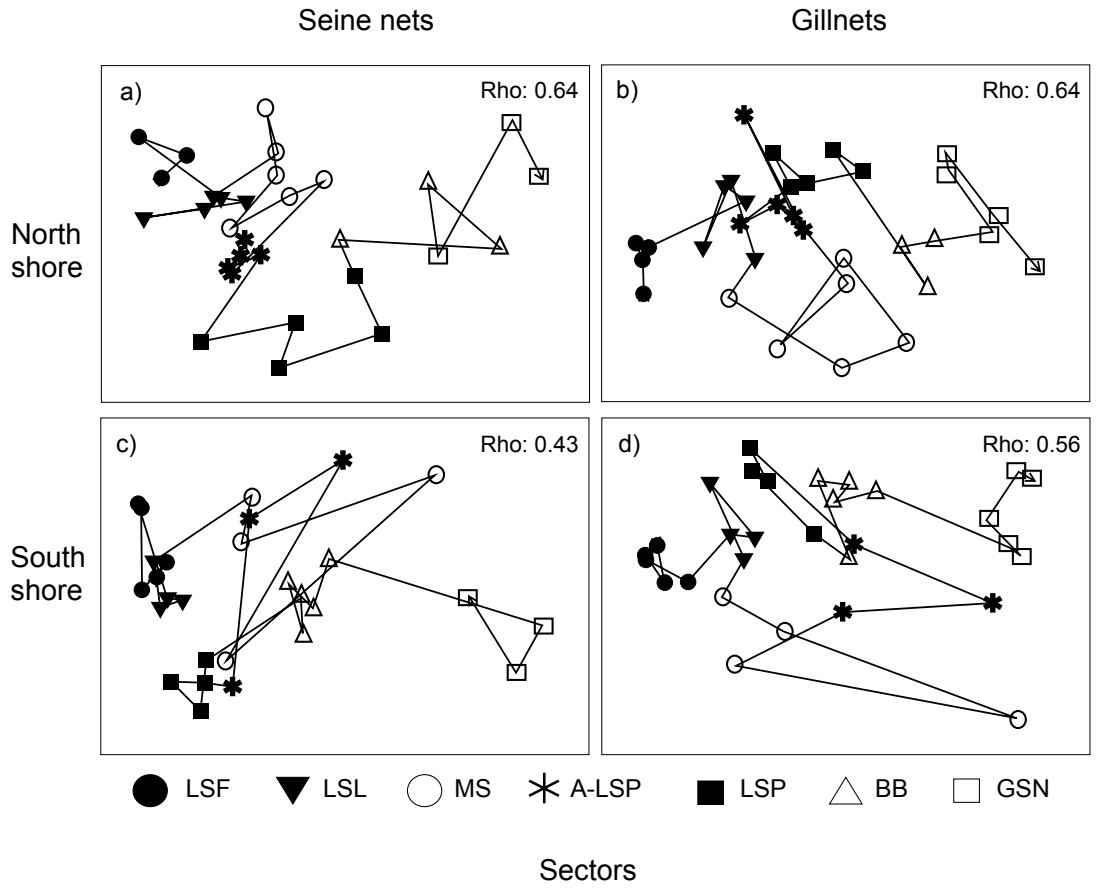

Figure A.2 Non-metric multidimensional scaling (nMDS) ordination plots representing sequential changes in segments of each sector for seine nets (a, c) and gillnets (b, d) upstream to downstream along the north and south shores of the St. Lawrence River. The lines indicate successive segments along the river (upstream to downstream) within hydro-morphological units. Reading across rows, stress values =0.15, 0.12, 0.14, 0.09.

The index of multivariate seriation (IMS; RELATE procedure in PRIMER) reveals that fish communities' changes along the St. Lawrence River is significant in all case ($P \leq 0.007$) and follows a longitudinal gradient.

Table A.1 Number of samples and number of sites targeted in each sector by the RSI ("Réseau de Suivi Ichtyologique") using seine nets and gillnets. All sites were embedded in ecological segments dividing each sector.

SECTORS	Gears	Samples	Sites	Ecological segments
Lake Saint-François (LSF)	Seine nets	163	62	8
	Gillnets	198	71	9
Lake Saint-Louis (LSL)	Seine nets	236	98	9
	Gillnets	222	78	
Montréal-Sorel (MS)	Seine nets	115	115	10
	Gillnets	79	79	
Archipelago of Lake Saint-Pierre (A-LSP)	Seine nets	176	72	8
	Gillnets	187	76	
Lake Saint-Pierre (LSP)	Seine nets	155	63	9
	Gillnets	238	100	
Becancour-Batiscan (BB)	Seine nets	179	56	8
	Gillnets	231	64	
Grondines-Saint-Nicolas (GSN)	Seine nets	103	53	6
	Gillnets	104	64	10
Total	Seine nets	1 127	519	63
	Gillnets	1 259	532	
	All	2 386	1,051	

Table A.2 Average ($\bar{x} \pm$ SD) abundance of each species sampled by seine nets (a) and gillnets (b) in the RSI ("Réseau de Suivi Ichtyologique") from 1995 to 2012 in each sectors targeted of the St. Lawrence River. A total of 71 species from 24 families were collected by seine nets while a total of 45 species from 20 families were collected by gillnets. It appears that no sector is home to all species captured at the river scale.

a)

			LSF	LSL	MS	A-LSP	LSP	BB	GSN	Total
Number of samples			163	236	115	176	155	179	103	1127
Order	**Family**	**Species**	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
Acipenseriformes	Acipenseridae	*Acipenser fulvescens*	- -	- -	0.2 ± 0.1	- -	- -	0.1 ± 0.1	- -	0.4 ± 0.7
Amiiformes	Amiidae	*Amia calva*	- -	- -	0.9 ± 0.9	0.2 ± 0.1	- -	- -	- -	0.4 ± 0.6
Anguilliformes	Anguillidae	*Anguilla rostrata*	- -	0.8 ± 0.9	- -	- -	- -	- -	- -	0.2 ± 0.4
Atheriniformes	Atherinopsidae	*Labidesthes sicculus*	44.6 ± 29.9	13.8 ± 38.3	0.4 ± 2.5	1.9 ± 7.3	5.2 ± 13.8	0.5 ± 1.9	- -	1.4 ± 112.8
Clupeiformes	Clupeidae	*Alosa pseudoharengus*	0.4 ± 1.5	4.2 ± 25.3	2.1 ± 5.3	3.1 ± 7.9	0.2 ± 1.5	2.6 ± 8.5	2.8 ± 12.7	2.3 ± 13.2
		Alosa sapidissima	- -	0.3 ± 0.3	0.9 ± 0.5	0.4 ± 2.5	0.3 ± 0.2	0.7 ± 2.4	1.3 ± 2.8	0.3 ± 1.7
		Dorosoma cepedianum	- -	- -	- -	- -	- -	0.6 ± 0.7	0.2 ± 0.1	0.3 ± 0.5
Cypriniformes	Catostomidae	*Catostomus catostomus*	- -	- -	- -	0.6 ± 0.8	0.1 ± 0.2	0.6 ± 0.7	0.8 ± 0.4	0.2 ± 0.1
		Catostomus commersonii	0.2 ± 0.8	0.3 ± 0.9	2.9 ± 1.2	2.0 ± 4.2	0.2 ± 0.8	1.7 ± 4.2	0.2 ± 0.8	1.2 ± 4.1
		Carpiodes cyprinus	- -	0.4 ± 0.7	0.4 ± 1.6	0.4 ± 3.4	- -	0.2 ± 1.5	- -	0.1 ± 1.4
		Moxostoma anisurum	0.4 ± 0.3	0.5 ± 0.3	0.6 ± 3.6	0.6 ± 1.6	0.1 ± 0.2	0.5 ± 0.3	- -	0.2 ± 1.4
		Moxostoma macrolepidotum	0.6 ± 0.4	0.7 ± 0.4	4.5 ± 11.1	2.6 ± 4.5	0.3 ± 1.8	1.3 ± 6.2	0.4 ± 1.2	1.2 ± 5.0
		Moxostoma valenciennesi	- -	0.4 ± 0.7	0.9 ± 0.9	- -	- -	- -	- -	0.2 ± 0.4
	Cyprinidae	*Cyprinus carpio*	- -	0.3 ± 0.2	0.2 ± 1.0	0.3 ± 0.8	0.5 ± 0.2	0.2 ± 0.9	0.3 ± 0.2	0.1 ± 0.6
		Cyprinella spiloptera	0.6 ± 0.8	1.6 ± 7.9	3.5 ± 12.4	0.5 ± 4.7	0.4 ± 1.5	0.3 ± 1.7	- -	0.9 ± 5.8
		Exoglossum maxillingua	- -	- -	0.4 ± 0.4	- -	- -	- -	- -	0.4 ± 0.1
		Hybognathus regius	- -	- -	0.9 ± 4.7	29.4 ± 264.9	0.2 ± 1.4	0.8 ± 0.5	- -	4.8 ± 15.0
		Luxilus cornutus	- -	0.8 ± 0.9	0.1 ± 0.8	- -	- -	0.8 ± 0.6	- -	0.3 ± 0.3
		Notropis atherinoides	0.2 ± 0.2	2.6 ± 11.4	4.4 ± 13.6	35.0 ± 67.7	4.3 ± 13.7	4.3 ± 11.8	1.9 ± 6.1	7.8 ± 3.7
		Notropis bifrenatus	0.2 ± 2.3	0.6 ± 3.7	0.9 ± 8.1	7.7 ± 31.4	35.0 ± 84.4	0.1 ± 1.3	- -	6.2 ± 35.7
		Notemigonus crysoleucas	3.6 ± 14.9	12.4 ± 39.4	7.5 ± 33.4	23.4 ± 57.2	37.3 ± 77.0	2.5 ± 9.2	- -	13.9 ± 44.1
		Notropis heterodon	0.8 ± 4.7	1.3 ± 8.2	0.9 ± 0.9	0.2 ± 1.6	1.6 ± 8.3	0.1 ± 0.2	- -	0.7 ± 5.2
		Notropis heterolepis	0.4 ± 0.3	4.3 ± 56.7	- -	0.1 ± 1.3	2.1 ± 11.8	0.8 ± 1.0	- -	1.2 ± 26.3
		Notropis hudsonius	1.7 ± 5.2	5.3 ± 16.9	12.9 ± 3.3	17.3 ± 2.6	1.1 ± 3.6	3.3 ± 9.0	0.4 ± 1.5	6.8 ± 16.6
		Notropis rubellus	- -	0.4 ± 2.5	- -	- -	0.3 ± 0.3	0.9 ± 12.5	- -	0.2 ± 5.7
		Notropis stramineus	128.7 ± 657.9	5.3 ± 41.6	0.5 ± 1.9	0.7 ± 5.5	0.3 ± 2.3	0.2 ± 0.2	- -	19.9 ± 254.2
		Notropis volucellus	179.7 ± 1299.4	37.2 ± 348.4	33.2 ± 166.6	1.9 ± 28.8	3.8 ± 19.8	3.2 ± 17.6	- -	39.9 ± 524.2
		Pimephales notatus	2.8 ± 46.8	55.6 ± 158.7	39.6 ± 11.2	9.6 ± 3.3	28.9 ± 242.2	3.9 ± 12.8	1.0 ± 1.0	24.8 ± 124.2
		Pimephales promelas	- -	0.4 ± 0.7	- -	- -	0.6 ± 0.8	0.3 ± 3.8	- -	0.5 ± 1.5
		Rhinichthys cataractae	- -	- -	- -	0.6 ± 0.8	- -	- -	0.3 ± 0.3	0.4 ± 0.9
		Semotilus atromaculatus	- -	- -	0.9 ± 0.9	- -	- -	- -	- -	0.9 ± 0.3
		Semotilus corporalis	- -	0.6 ± 0.4	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 2.7	- -	0.7 ± 0.9
Cyprinodontiformes	Fundulidae	*Fundulus diaphanus*	9.3 ± 3.9	12.7 ± 2.5	25.0 ± 137.2	1.4 ± 6.6	66.3 ± 277.2	25.9 ± 89.0	28.2 ± 89.8	22.4 ± 122.5
Esociformes	Esocidae	*Esox americanus americanus*	- -	- -	- -	0.6 ± 0.8	- -	- -	- -	0.9 ± 0.3
		Esox lucius	0.2 ± 0.1	0.2 ± 0.6	0.7 ± 0.4	0.6 ± 2.4	0.2 ± 0.7	0.7 ± 0.3	0.2 ± 0.1	0.2 ± 1.5
		Esox masquinongy	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.5	0.6 ± 0.8	- -	0.2 ± 0.2	- -	0.2 ± 0.3
	Umbridae	*Umbra limi*	- -	0.4 ± 0.7	- -	- -	0.1 ± 0.1	- -	- -	0.3 ± 0.5
Gadiformes	Lotidae	*Lota lota*	- -	0.4 ± 0.7	- -	- -	- -	- -	- -	0.9 ± 0.3
Gasterosteiformes	Gasterosteidae	*Apeltes quadracus*	- -	- -	- -	- -	- -	0.1 ± 0.8	- -	0.2 ± 0.4
		Culaea inconstans	- -	0.3 ± 2.7	0.1 ± 0.7	- -	- -	0.4 ± 0.5	- -	0.7 ± 1.0
		Gasterosteus aculeatus	- -	- -	- -	- -	- -	0.6 ± 0.7	1.0 ± 1.0	0.2 ± 0.4
Lepisosteiformes	Lepisosteidae	*Lepisosteus osseus*	- -	0.3 ± 0.2	0.5 ± 0.6	0.6 ± 0.8	0.6 ± 0.8	0.6 ± 0.7	- -	0.1 ± 0.2
Osmeriformes	Osmeridae	*Osmerus mordax*	0.6 ± 0.8	0.6 ± 0.7	0.2 ± 1.1	0.3 ± 1.1	0.6 ± 0.8	0.4 ± 2.8	1.0 ± 0.5	0.1 ± 1.3
Osteoglossiformes	Hiodontidae	*Hiodon tergisus*	- -	- -	0.3 ± 1.4	0.1 ± 0.6	- -	0.2 ± 1.7	0.1 ± 1.2	0.9 ± 0.7
Perciformes	Centrarchidae	*Ambloplites rupestris*	2.8 ± 6.5	7.8 ± 12.3	6.8 ± 14.8	5.4 ± 1.9	0.6 ± 2.4	0.4 ± 1.1	0.3 ± 0.2	3.7 ± 9.4
		Lepomis gibbosus	5.4 ± 18.8	25.4 ± 54.2	11.8 ± 53.6	28.9 ± 46.2	22.8 ± 44.8	3.3 ± 24.8	0.2 ± 0.1	15.5 ± 42.1
		Lepomis macrochirus	- -	0.2 ± 0.7	- -	- -	- -	- -	- -	0.2 ± 0.3
		Micropterus dolomieu	0.2 ± 0.4	0.3 ± 0.6	0.7 ± 2.3	0.4 ± 1.0	0.3 ± 0.2	0.2 ± 0.9	0.5 ± 1.6	0.3 ± 1.9
		Micropterus salmoides	1.3 ± 3.3	1.7 ± 3.9	0.2 ± 0.7	0.8 ± 2.5	0.8 ± 0.3	0.6 ± 0.4	- -	0.7 ± 2.5
		Pomoxis nigromaculatus	0.2 ± 1.4	1.3 ± 7.4	1.0 ± 0.8	2.9 ± 7.6	0.4 ± 0.5	0.5 ± 0.2	- -	0.7 ± 4.5
	Gobiidae	*Neogobius melanostomus*	11.9 ± 26.3	6.6 ± 15.7	- -	0.8 ± 2.8	0.5 ± 3.2	3.9 ± 13.4	0.2 ± 2.4	3.9 ± 14.1
	Moronidae	*Morone americana*	0.4 ± 0.5	0.6 ± 0.7	0.2 ± 0.1	0.1 ± 0.2	- -	0.9 ± 0.6	0.2 ± 0.1	0.4 ± 0.4
		Morone saxatilis	- -	- -	- -	- -	- -	0.1 ± 0.1	- -	0.2 ± 0.6
	Percidae	*Ammocrypta pellucida*	- -	- -	0.9 ± 0.9	0.3 ± 0.2	0.4 ± 0.3	- -	- -	0.2 ± 0.2
		Etheostoma exile	0.4 ± 0.3	0.4 ± 2.5	- -	0.6 ± 0.8	0.1 ± 0.1	- -	- -	1.0 ± 1.2
		Etheostoma flabellare	- -	0.8 ± 0.1	- -	- -	- -	- -	- -	0.2 ± 0.6
		Etheostoma nigrum	0.1 ± 0.6	0.5 ± 0.3	0.1 ± 0.7	0.8 ± 2.3	0.2 ± 0.8	0.4 ± 0.2	- -	0.2 ± 1.5
		Etheostoma olmstedi	8.5 ± 19.9	7.6 ± 17.2	16.3 ± 41.4	19.5 ± 26.9	8.2 ± 12.5	4.6 ± 9.9	3.5 ± 9.2	9.6 ± 21.7
		Percina caprodes	1.0 ± 2.9	4.7 ± 12.2	8.9 ± 33.6	2.3 ± 5.2	0.9 ± 2.3	0.9 ± 3.3	1.4 ± 4.6	2.8 ± 12.8
		Percina copelandi	0.6 ± 0.8	- -	- -	0.2 ± 1.8	0.8 ± 2.5	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 1.6
		Perca flavescens	8.2 ± 15.6	11.4 ± 17.9	11.3 ± 27.7	32.4 ± 42.7	9.6 ± 14.2	19.9 ± 58.9	0.6 ± 3.5	14.2 ± 33.4
		Sander canadensis	- -	0.4 ± 0.7	0.3 ± 0.2	0.5 ± 0.2	- -	0.2 ± 0.1	1.0 ± 1.0	0.2 ± 0.1
		Sander vitreus	0.2 ± 0.1	0.9 ± 0.6	0.4 ± 1.1	0.4 ± 0.8	0.5 ± 0.3	0.1 ± 0.5	0.1 ± 0.4	0.2 ± 0.6
	Sciaenidae	*Aplodinotus grunniens*	- -	- -	- -	0.3 ± 0.2	- -	- -	- -	0.4 ± 0.8
Percopsiformes	Percopsidae	*Percopsis omiscomaycus*	0.6 ± 0.8	0.2 ± 3.0	7.1 ± 34.0	9.7 ± 29.4	1.0 ± 6.9	1.2 ± 4.4	2.0 ± 4.3	2.7 ± 16.6
Petromyzontiformes	Petromyzontidae	*Ichthyomyzon unicuspis*	0.6 ± 0.8	- -	- -	- -	- -	- -	- -	0.9 ± 0.3
Scorpaeniformes	Cottidae	*Cottus bairdii*	0.6 ± 0.8	0.3 ± 0.3	0.9 ± 0.9	- -	- -	- -	- -	0.9 ± 0.2
Siluriformes	Ictaluridae	*Ameiurus nebulosus*	0.9 ± 0.5	0.4 ± 1.4	0.4 ± 1.9	9.0 ± 61.8	5.2 ± 26.7	0.2 ± 1.5	- -	2.3 ± 26.5
		Ictalurus punctatus	- -	- -	0.9 ± 0.9	0.6 ± 0.8	0.6 ± 0.8	- -	- -	0.3 ± 0.5
		Noturus flavus	- -	- -	- -	- -	- -	0.6 ± 0.7	- -	0.9 ± 0.3
		Noturus gyrinus	0.6 ± 0.8	0.7 ± 0.5	- -	0.7 ± 0.3	0.2 ± 0.7	0.1 ± 0.2	- -	0.6 ± 0.4

b)

			LSF	LSL	MS	A-LSP	LSP	BB	GSN	Total
Number of samples			198	222	79	187	238	231	104	1259
Order	**Family**	**Species**	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
Acipenseriformes	Acipenseridae	*Acipenser fulvescens*	0.4 ± 0.2	1.9 ± 3.6	1.1 ± 1.7	0.8 ± 1.8	0.8 ± 1.7	1.8 ± 3.0	2.7 ± 4.6	1.3 ± 2.7
		Acipenser oxyrinchus	- -	- -	- -	- -	- -	0.4 ± 0.7	1.0 ± 1.0	0.2 ± 0.4
Amiiformes	Amiidae	*Amia calva*	- -	0.1 ± 0.1	- -	0.2 ± 0.8	0.1 ± 0.1	0.1 ± 0.1	- -	0.3 ± 0.3
Clupeiformes	Clupeidae	*Alosa pseudoharengus*	0.2 ± 0.6	0.2 ± 1.8	- -	0.1 ± 1.1	0.4 ± 2.6	0.4 ± 0.7	0.4 ± 1.1	0.2 ± 1.5
		Alosa sapidissima	- -	0.1 ± 0.6	- -	1.3 ± 9.3	0.3 ± 1.8	0.5 ± 2.4	- -	0.4 ± 3.8
		Dorosoma cepedianum	- -	- -	- -	0.3 ± 0.2	- -	- -	- -	0.5 ± 0.9
Cypriniformes	Catostomidae	*Catostomus catostomus*	- -	- -	0.1 ± 0.5	0.5 ± 0.7	0.2 ± 0.9	0.1 ± 0.5	3.3 ± 4.5	0.3 ± 1.6
		Catostomus commersonii	1.3 ± 1.7	1.9 ± 1.7	0.7 ± 1.3	0.7 ± 1.3	3.4 ± 3.6	1.1 ± 2.0	1.7 ± 2.1	1.5 ± 2.4
		Carpiodes cyprinus	- -	0.9 ± 0.6	- -	0.2 ± 0.7	- -	0.9 ± 0.1	- -	0.4 ± 0.4
		Moxostoma anisurum	0.6 ± 0.3	0.6 ± 1.3	0.1 ± 0.4	0.2 ± 0.7	0.6 ± 1.3	0.6 ± 1.0	1.0 ± 1.0	0.4 ± 0.9
		Moxostoma macrolepidotum	1.0 ± 0.6	0.8 ± 1.8	0.8 ± 1.2	1.5 ± 2.4	3.2 ± 4.1	3.2 ± 5.9	2.2 ± 3.3	1.8 ± 3.7
	Cyprinidae	*Cyprinus carpio*	0.2 ± 0.2	0.4 ± 1.4	0.2 ± 0.8	0.6 ± 1.0	0.4 ± 1.3	2.0 ± 3.1	0.2 ± 0.1	0.4 ± 1.6
		Hybognathus regius	- -	- -	- -	0.5 ± 0.6	0.8 ± 0.1	- -	- -	1.0 ± 0.2
		Notemigonus crysoleucas	0.8 ± 4.4	0.4 ± 2.7	0.9 ± 0.7	2.4 ± 1.4	1.5 ± 5.7	2.0 ± 13.6	- -	1.3 ± 7.8
		Notropis hudsonius	2.0 ± 7.8	0.6 ± 2.9	0.6 ± 0.3	0.1 ± 0.5	0.8 ± 2.8	0.2 ± 2.0	- -	0.6 ± 3.5
		Semotilus corporalis	0.6 ± 0.7	- -	- -	- -	- -	- -	- -	0.8 ± 0.3
Esociformes	Esocidae	*Esox lucius*	1.9 ± 2.4	1.7 ± 3.2	0.6 ± 1.6	1.4 ± 2.3	2.3 ± 3.5	0.8 ± 2.2	- -	1.4 ± 2.8
		Esox masquinongy	0.6 ± 0.7	0.5 ± 0.2	0.1 ± 0.1	- -	0.4 ± 0.6	0.4 ± 0.4	- -	0.2 ± 0.2
Gadiformes	Gadidae	*Microgadus tomcod*	- -	- -	- -	- -	- -	- -	1.0 ± 1.0	0.8 ± 0.3
	Lotidae	*Lota lota*	- -	- -	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	1.0 ± 1.0	0.1 ± 0.1
Lepisosteiformes	Lepisosteidae	*Lepisosteus osseus*	0.3 ± 0.2	0.1 ± 0.5	- -	0.5 ± 0.7	0.4 ± 0.6	- -	- -	0.3 ± 0.2
Osmeriformes	Osmeridae	*Osmerus mordax*	- -	- -	- -	0.5 ± 0.7	- -	- -	- -	0.8 ± 0.3
Osteoglossiformes	Hiodontidae	*Hiodon tergisus*	- -	1.3 ± 4.9	0.6 ± 0.4	1.3 ± 3.3	1.6 ± 3.8	0.4 ± 1.3	0.3 ± 0.2	0.9 ± 3.4
Perciformes	Centrarchidae	*Ambloplites rupestris*	8.4 ± 1.4	4.5 ± 5.9	1.7 ± 2.6	1.0 ± 1.5	0.5 ± 1.2	0.5 ± 0.9	1.0 ± 1.0	2.5 ± 5.7
		Lepomis gibbosus	0.9 ± 1.9	0.7 ± 2.9	0.4 ± 0.3	0.2 ± 0.6	0.3 ± 0.7	0.4 ± 0.7	- -	0.4 ± 1.3
		Lepomis macrochirus	0.6 ± 0.7	- -	- -	- -	- -	- -	- -	0.8 ± 0.3
		Micropterus dolomieu	1.2 ± 2.8	1.8 ± 2.7	0.7 ± 1.4	0.6 ± 1.1	0.4 ± 1.0	0.8 ± 1.6	0.3 ± 0.7	0.9 ± 1.9
		Micropterus salmoides	0.5 ± 1.5	0.4 ± 1.5	- -	0.2 ± 0.9	0.4 ± 0.2	0.2 ± 0.1	- -	0.2 ± 0.9
		Pomoxis nigromaculatus	0.8 ± 0.4	0.2 ± 0.1	- -	0.2 ± 0.8	- -	0.3 ± 0.2	- -	0.5 ± 0.4
	Gobiidae	*Neogobius melanostomus*	0.8 ± 0.3	0.2 ± 0.3	- -	0.2 ± 0.1	0.8 ± 0.3	0.2 ± 0.1	- -	0.3 ± 0.2
	Moronidae	*Morone americana*	- -	0.4 ± 0.2	0.1 ± 0.1	0.3 ± 1.7	0.7 ± 0.3	0.3 ± 1.3	0.2 ± 0.5	0.1 ± 0.9
		Morone saxatilis	- -	- -	- -	- -	- -	0.1 ± 0.1	- -	0.2 ± 0.6
	Percidae	*Percina caprodes*	- -	1.0 ± 0.9	- -	0.2 ± 0.1	0.8 ± 0.4	0.1 ± 0.1	- -	0.2 ± 0.2
		Perca flavescens	34.5 ± 31.3	43.4 ± 65.9	4.4 ± 7.0	7.9 ± 1.5	17.8 ± 24.8	5.8 ± 11.9	0.1 ± 0.4	18.8 ± 36.3
		Sander canadensis	- -	0.8 ± 3.0	0.8 ± 1.2	1.9 ± 2.4	1.7 ± 2.7	2.5 ± 3.4	5.6 ± 6.8	1.7 ± 3.7
		Sander vitreus	0.8 ± 1.2	5.4 ± 6.8	1.5 ± 1.5	2.9 ± 2.7	4.2 ± 3.7	2.9 ± 3.3	2.5 ± 2.5	3.8 ± 4.0
	Sciaenidae	*Aplodinotus grunniens*	- -	0.5 ± 0.3	- -	0.7 ± 0.3	0.3 ± 0.2	0.4 ± 0.7	1.0 ± 1.0	0.3 ± 0.2
Percopsiformes	Percopsidae	*Percopsis omiscomaycus*	- -	0.5 ± 0.7	- -	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.7	- -	0.7 ± 0.8
Petromyzontiformes	Petromyzontidae	*Ichthyomyzon unicuspis*	- -	0.6 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	1.0 ± 1.0	0.2 ± 0.2
Salmoniformes	Salmonidae	*Coregonus clupeaformis*	- -	- -	- -	- -	0.4 ± 0.3	- -	1.0 ± 1.0	0.8 ± 0.1
		Onchorhynchus kisutch	0.6 ± 0.7	- -	- -	- -	- -	- -	- -	0.8 ± 0.3
		Oncorhynchus tshawytscha	0.6 ± 0.7	- -	- -	0.5 ± 0.7	- -	- -	- -	0.2 ± 0.4
Siluriformes	Ichtaluridae	*Ameiurus nebulosus*	0.3 ± 0.7	0.3 ± 1.0	0.2 ± 0.7	2.8 ± 6.9	3.2 ± 9.7	0.4 ± 1.5	- -	1.2 ± 5.3
		Ictalurus punctatus	- -	0.4 ± 0.9	0.5 ± 1.3	0.5 ± 1.8	1.3 ± 2.3	1.3 ± 3.9	1.6 ± 2.5	0.7 ± 2.3
		Noturus flavus	- -	- -	- -	- -	- -	0.4 ± 0.7	- -	0.8 ± 0.3

Table A.3 Indicator species of the overall fish communities captured by seine nets and gillnets in the St. Lawrence River (IndVal analysis; Dufrene et Legendre 1997). Significance was tested using a random permutation procedure.

Species	Seine nets	Gillnets
Acipenser fulvescens		■
Alosa pseudoharengus	■	
Aplodinotus grunniens		■
Catostomus catostomus		■
Culaea inconstans	■	
Cyprinella spiloptera	■	
Esox lucius		■
Etheostoma exile	■	
Etheostoma nigrum	■	
Etheostoma olmstedi	■	
Fundulus diaphanus	■	
Hiodon tergisus		■
Hybognathus regius	■	
Ictalurus punctatus		■
Ichthyomyzon unicuspis		■
Labidesthes sicculus	■	
Lepomis gibbosus	■	
Lota lota		■
Negobius melanostomus	■	
Notropis atherinoides	■	
Notropis bifrenatus	■	
Notemigonus crysoleucas	■	
Noturus gyrinus	■	
Notropis heterodon	■	
Notropis heterolepis	■	
Notropis hudsonius	■	
Notropis rubellus	■	
Notropis stramineus	■	
Notropis volucellus	■	
Osmerus mordax	■	
Percina caprodes	■	
Percina copelandi	■	
Percopsis omiscomaycus	■	
Pimephales notatus	■	
Sander canadensis		■
Sander vitreus		■
Semotilus corporalis	■	

Table A.4 Average dissimilarity (Bray-Curtis, log-transformed abundance) among sectors for fish communities collected by seine nets (a) and gillnets (b).

a)

SECTORS	Lake Saint-François (LSF)	Lake Saint-Louis (LSL)	Montréal-Sorel (MS)	Archipelago of Lake Saint-Pierre (A-LSP)	Lake Saint-Pierre (LSP)	Bécancour-Batiscan (BB)
Lake Saint-Louis (LSL)	33.16					
Montréal-Sorel (MS)	47.26	43.55				
Archipelago of Lake Saint-Pierre (A-LSP)	47.80	40.18	39.98			
Lake Saint-Pierre (LSP)	49.14	44.72	50.21	44.35		
Bécancour-Batiscan (BB)	48.04	42.28	40.82	40.24	46.86	
Grondines-Saint-Nicolas (GSN)	70.52	66.54	56.12	62.01	63.36	52.08

b)

SECTORS	Lake Saint-François (LSF)	Lake Saint-Louis (LSL)	Montréal-Sorel (MS)	Archipelago of Lake Saint-Pierre (A-LSP)	Lake Saint-Pierre (LSP)	Bécancour-Batiscan (BB)
Lake Saint-Louis (LSL)	35.38					
Montréal-Sorel (MS)	56.52	54.69				
Archipelago of Lake Saint-Pierre (A-LSP)	51.95	38.97	55.48			
Lake Saint-Pierre (LSP)	44.87	30.74	57.56	36.98		
Bécancour-Batiscan (BB)	54.28	34.96	53.57	38.53	29.66	
Grondines-Saint-Nicolas (GSN)	74.21	61.02	57.72	58.65	55.94	49.61

Table A.5 Indicator species (black boxes) in each seven sectors captured by seine nets (a) and gillnets (b) in the St. Lawrence River (IndVal analysis; Dufrene et Legendre 1997). Species followed by "*" are indicators of only one sector. Significance was tested using a random permutation procedure and the "Holm" adjustment method (Holm 1979) was used to correct for multiple testing (De Cáceres *et al.* 2010).

a)

	Lake Saint-François (LSF)	Lake Saint-Louis (LSL)	Montréal-Sorel (MS)	Archipelago of Lake Saint-Pierre (A-LSP)	Lake Saint-Pierre (LSP)	Becancour-Batiscan (BB)	Grondines-Saint-Nicolas (GSN)
Hybognathus regius *				■			
Percina copelandi				■	■		
Notemigonus bifrenatus				■	■		
Ameiurus nebulosus		■		■	■		
Esox lucius		■		■	■	■	
Notropis atheriniodes		■	■	■	■	■	■
Percopsis omiscomaycus			■	■	■	■	■
Alosa sapidissima				■		■	■
Carpiodes cyprinus			■	■		■	
Cyprinus carpio			■	■		■	
Notropis volucellus	■	■	■	■		■	
Lepomis gibbosus	■	■	■	■	■	■	
Notemigonus crysoleucas	■	■	■	■	■	■	
Perca flavescens	■	■	■	■	■	■	
Pimephales notatus	■	■	■	■	■		
Ambloplites rupestris	■	■	■	■			
Labidesthes sicculus	■	■		■	■		
Micropterus salmoides	■	■		■			
Neogobius melanostomus	■	■				■	
Notropis stramineus *	■						
Apeltes quadracus *						■	

b)

	Lake Saint-François (LSF)	Lake Saint-Louis (LSL)	Montréal-Sorel (MS)	Archipelago of Lake Saint-Pierre (A-LSP)	Lake Saint-Pierre (LSP)	Becancour-Batiscan (BB)	Grondines-Saint-Nicolas (GSN)
Esox masquinongy		■				■	
Morone americana				■		■	
Pomoxis nigromaculatus	■			■		■	
Neogobius melanostomus	■				■		
Coregonus clupeaformis *					■		
Catostomus catostomus					■	■	■
Sander canadensis		■		■	■	■	■
Moxostoma macrolepidotum		■		■	■	■	■
Ictalurus punctatus		■		■	■	■	■
Alosa pseudoharengus	■	■		■	■		■
Catostomus commersonii	■	■		■	■	■	■
Acipenser fulvescens		■	■	■	■	■	■
Ambloplites rupestris	■	■	■	■	■	■	
Micropterus dolomieu	■	■	■	■	■	■	
Ameiurus nebulosus	■	■		■	■	■	
Esox lucius	■	■		■	■	■	
Notemigonus crysoleucas	■	■		■	■	■	
Perca flavescens	■	■		■	■	■	
Cyprinus carpio		■		■	■	■	
Hiodon tergisus		■		■	■	■	
Moxostoma anisurum		■		■	■	■	
Alosa sapidissima				■	■	■	
Aplodinotus grunniens		■		■	■		
Lepomis gibbosus	■	■		■	■		
Micropterus salmoides	■	■		■			
Notropis hudsonius	■	■			■		
Lepisosteus osseus	■	■					
Carpiodes cyprinus		■		■			
Amia calva *				■			

Table A.6 Indicator species in the two opposing shores captured by seine nets (a) and gillnets (b) in the St. Lawrence River (IndVal analysis; Dufrene et Legendre, 1997). Significance was tested using a random permutation procedure. The analysis was performed only for sectors where the structure of fish communities was significantly different between north and south shores.

a)

Species	Lake Saint-Louis (LSL)		Lake Saint-Pierre (LSP)		Becancour-Batiscan (BB)	
	North	South	North	South	North	South
Apeltes quadracus						
Carpiodes cyprinus						
Cyprinella spiloptera						
Fundulus diaphanus						
Labidesthes sicculus						
Micropterus dolomieu						
Notropis heterodon						
Notropis heterolepis						
Notropis rubellus						
Notropis volucellus						
Pimephales notatus						

b)

Species	Archipelago of Lake Saint-Pierre (A-LSP)		Lake Saint-Pierre (LSP)		Becancour-Batiscan (BB)	
	North	South	North	South	North	South
Ameiurus nebulosus						
Amia calva						
Cyprinus carpio						
Esox lucius						
Hiodon tergisus						
Lepomis gibbosus						
Morone americana						
Notemigonus crysoleucas						
Perca flavescens						
Percina caprodes						
Pomoxis nigromaculatus						

APPENDICE B

CHAPITRE II

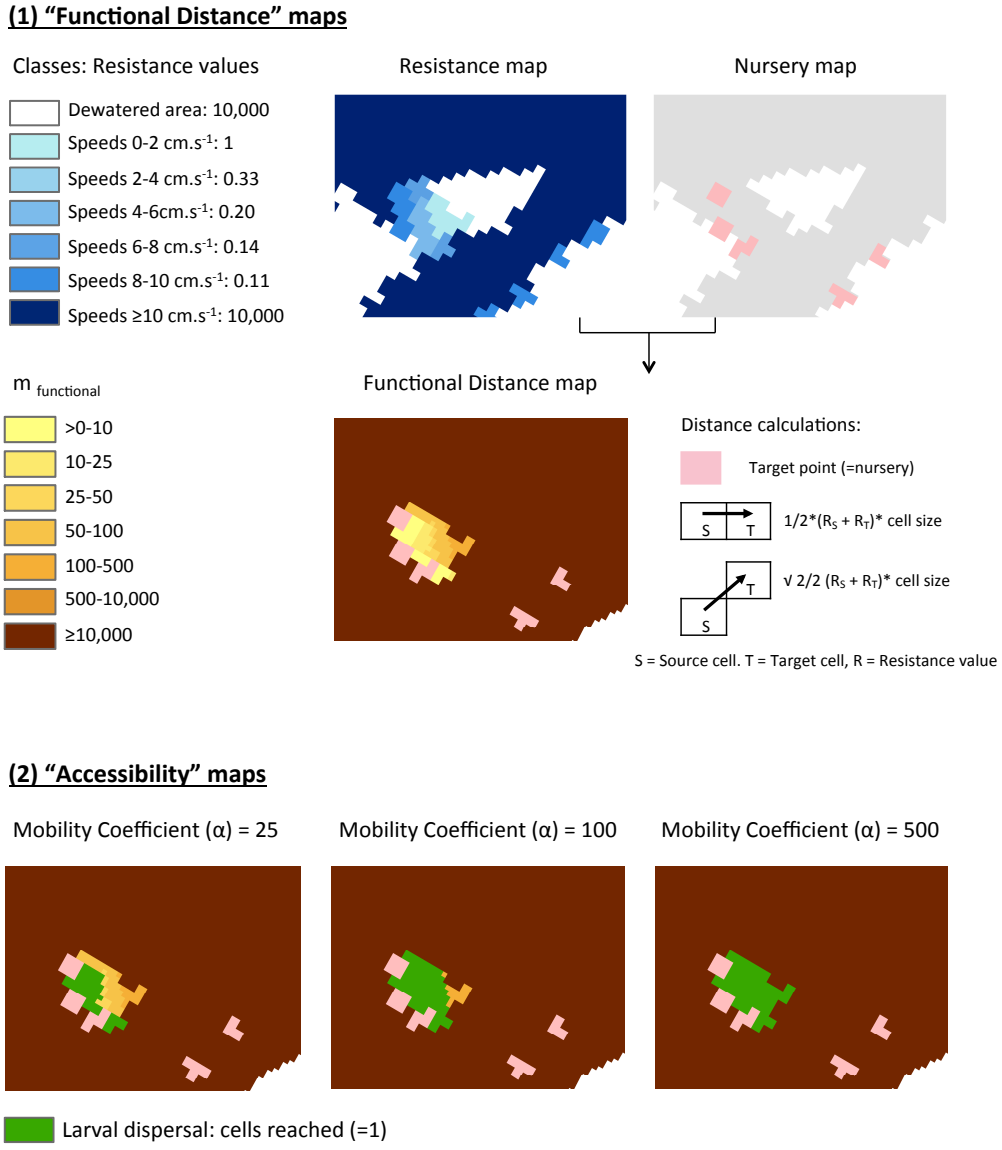

Figure B.1 Illustration of functional distance calculation and the use of mobility coefficient to generate accessibility maps in *Anaqualand* 2.0. An island located in the Montréal-Sorel corridor during the decreasing profile between the maximum spawning time ($Week_0$) and the beginning of free-swimming stage ($Week_5$) observed in spring 1998 was used to illustrate the different steps of the calculation.

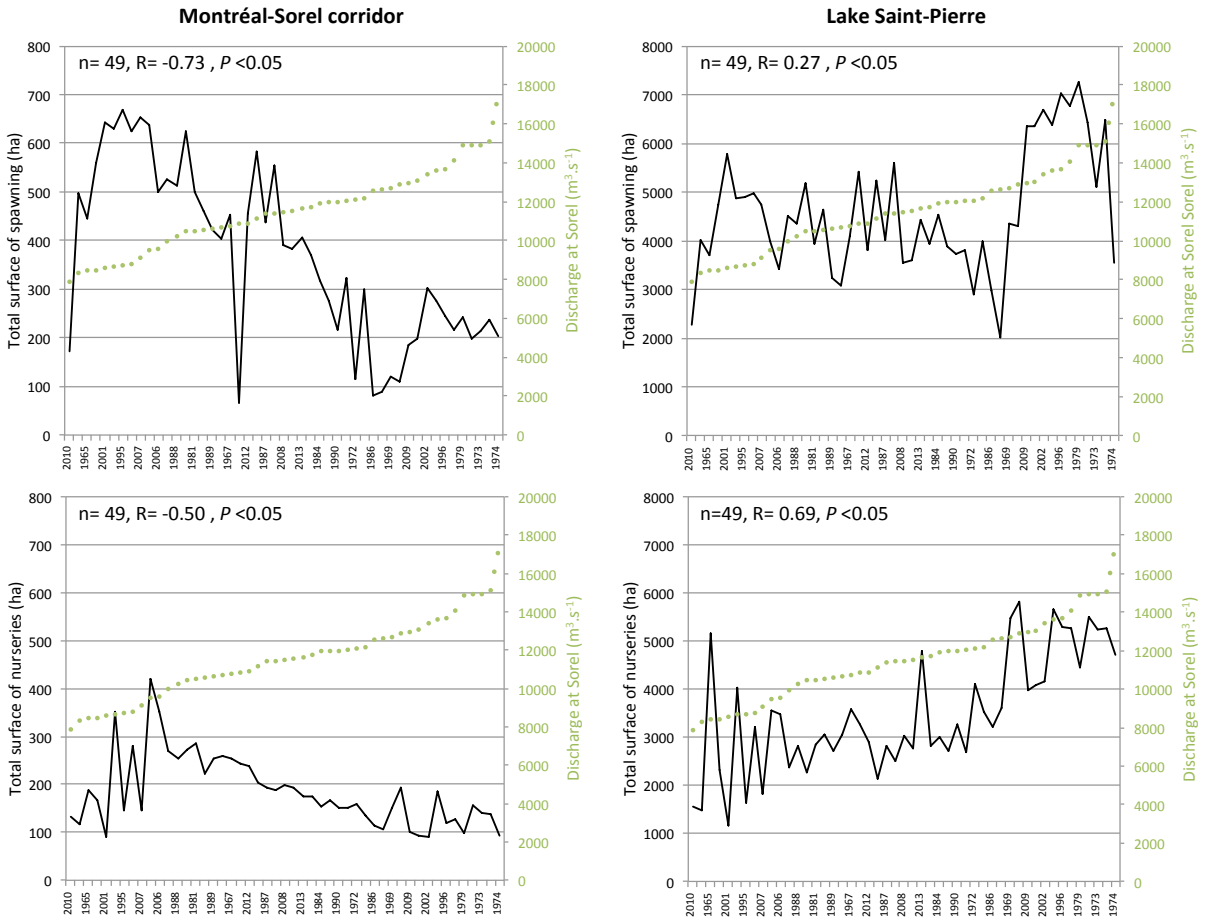

Figure B.2 Relation between the total surface of spawning and nursery habitats (solid lines) with the water discharge during the maximum spawning time ($Week_0$) and the beginning of free-swimming stage ($Week_5$, green points) in the Montréal-Sorel corridor and the Lake Saint-Pierre during the period 1965-2013 (all four P <0.05, Spearman's rank correlation). Although high water discharges generate larger potential spawning and nursery areas in the Lake Saint-Pierre (positive correlation), the same hydrological condition resulted in smaller surface areas of habitats available in the Montréal-Sorel corridor (negative correlation).

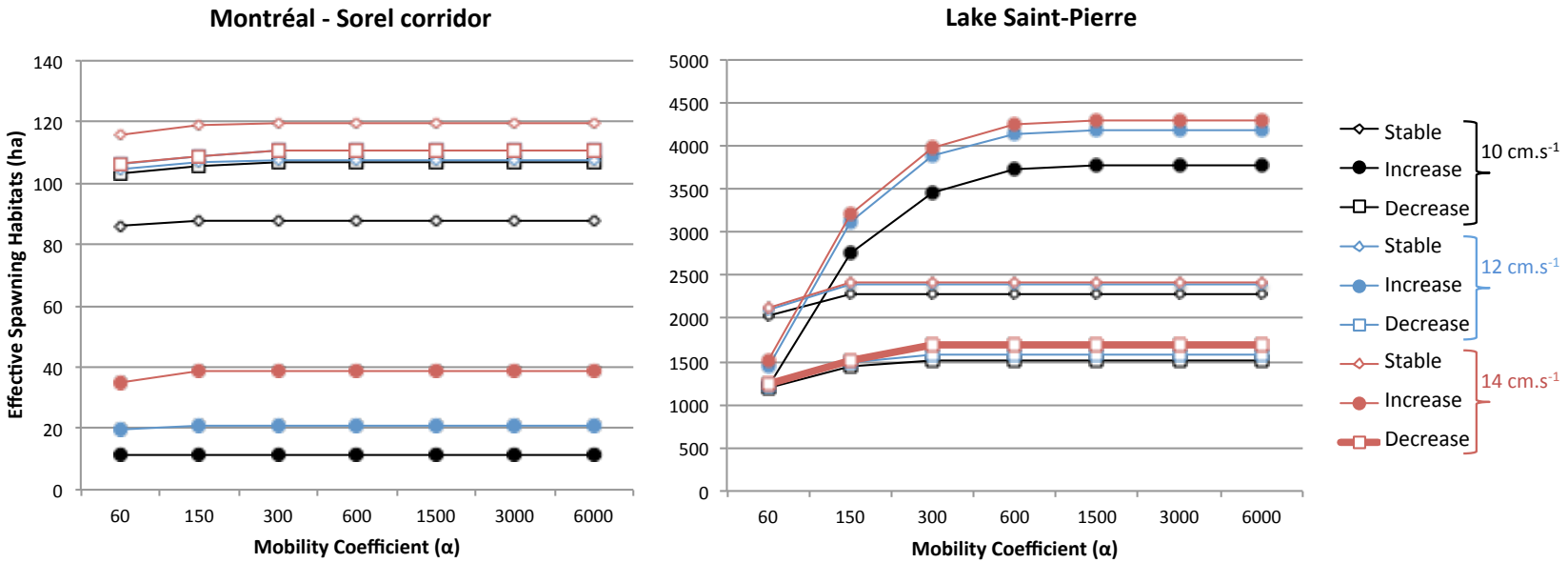

Figure B.3 Sensitivity analysis of the current velocity thresholds (10 cm.s^{-1}, 12 cm.s^{-1}, 14 cm.s^{-1}) in both contrasted regions studied in the St. Lawrence River for the three profile selected (stable in 1965, increase in 1983, decrease in 1998).

Table B.1 Values of the resistance map classes (dimensionless) based on dewatering between the maximum spawning time ($Week_0$) and the beginning of free-swimming stage ($Week_5$) as well as current speeds simulated at $Week_5$.

Resistance map classes ($cm.s^{-1}$)	**Mean ($cm.s^{-1}$)**	**Potential distance covered by a passive particle (m/week)**	**Downstream resistance value**				**Upstream resistance value**	
			Threshold 10 $cm.s^{-1}$	**Threshold 12 $cm.s^{-1}$**	**Threshold 14 $cm.s^{-1}$**	**No facilitation**	**Threshold 2 $cm.s^{-1}$**	**No movements**
1: ≤ 0 and dewatering between W_0-W_5	0	0	10,000	10,000	10,000	10,000	10,000	10,000
2: > 0 ≤ 2	1	6,048 *	1	1	1	1	1	10,000
3: > 2 ≤ 4	3 **	18,144	0.3333	0.3333	0.3333	1	10,000	10,000
4: > 4 ≤ 6	5	30,240	0.2000	0.2000	0.2000	1	10,000	10,000
5: > 6 ≤ 8	7	42,336	0.1429	0.1429	0.1429	1	10,000	10,000
6: > 8 ≤ 10	9	54,432	0.1111	0.1111	0.1111	1	10,000	10,000
7: > 10 ≤ 12	11	66,528	10,000	0.0909	0.0909	10,000	10,000	10,000
8: > 12 ≤ 14	13	78,624	10,000	10,000	0.0769	10,000	10,000	10,000
9: > 20	21	120,960	10,000	10,000	10,000	10,000	10,000	10,000

* If the current speed is equal in average to 1 $cm.s^{-1}$, the passive particle will travel 6,048 m/week: 1 $cm.s^{-1}$ = 864 m/day (36x24) = 6,048 m/week (864 x 7). ** We considered that larvae transport by currents was three times faster in the class 2-4 $cm.s^{-1}$ (mean value of 3 $cm.s^{-1}$) than in the class 0-2 $cm.s^{-1}$ (mean value of 1 $cm.s^{-1}$).

APPENDICE C

CHAPITRE III

Table C.1 Types of land-use identified in the Lake Saint-Pierre (St. Lawrence River, Canada) using aerial photographs for the years 1964 and 1997 (Richard *et al*. 2011), and satellite imagery for the year 2014 (Jobin et Dauphin in prep). We interpreted the various land-use types and assigned land use to six categories. While suitable wetlands, perennial crops and drainage ditches land-use categories are suitable for fish habitats, unsuitable wetlands and wooded, annual crops, and roads and urban areas categories have negatively altered the habitats in the Lake Saint-Pierre floodplain.

Themes	Categories	Types	ha	%
Agriculture	Drainage ditches	Uncultivated agricultural areas	743	0.83
		Wastelands	2028	2.27
		Agricultural ditches	15	0.02
	Non-perennial crops	Soja	8742	9.78
		Corn	7838	8.77
		Vegetable crops	800	0.90
		Wheat	804	0.90
		Bare soil	102	0.20
		Oat	313	0.35
		Other cereals	197	0.22
		Mixed crops	125	0.14
		Barley	248	0.28
	Perennial crops	Hay	1458	1.63
		Pasture/Forage crops	865	0.97
Roads	Roads and urban areas	Unpaved local road	54	0.06
		Paved local road	259	0.29
		Paved national road	207	0.23
		Paved collector road	44	0.05
		Highway	372	0.42
		Highway	3	0.00
		Highway connections	43	0.05
Urban		Urban areas	3713	4.15
		Airport	12	0.01
Water	Suitable wetlands	Rivers	747	0.84
		Shallow water	3205	3.59
		Lakes	20	0.02
		St. Lawrence River (deep water)	33536	48.34
Wetlands		Shrubby swamps	2820	3.15
		Wet meadow	2829	3.17
		Marshes	8344	9.34
Wooded	Unsuitable wetlands and wooded	Hardwood	1838	2.06
		Plantation	82	0.09
		Wooded mixed	389	0.44
		Resinous	154	0.17
Wetlands		Treed swamps	6293	7.04
		Open peat-bogs	45	0.05
		Wooded peat-bogs	82	0.09
SOMME			**89370**	100.00

Sensitivity analysis of the mobility coefficient (α) in the contemporary altered state of the Lake Saint-Pierre.

As in Foubert *et al*. (in prep, see chapter II in the present thesis), sensitivity analysis of the mobility coefficient (α) were performed in the contemporary state of the Lake Saint-Pierre. The mobility coefficient (α) is a measure reflecting the larval dispersal capacity across the landscape. The α value was derived from stage-specific larval swimming capacities and potential passive transport provided by local currents at the beginning of the free-swimming stage ($Week_5$). The maximal value was set to α =6,000 m which corresponds to the maximal distance travelled at 1 $cm.s^{-1}$ by a neutral particle in the water column over a period of one week in the St. Lawrence River. Since larvae can modulate the passive dispersal through behavior (e.g. selecting slower bottom currents, migrating in the water column, seeking refuge in vegetation or exploiting physical features reducing advection), we conducted sensitivity analysis using α values set at 3,000, 1,500, 600, 300, 150 and 60 m.

When α integrate the least-cost of moving in the different landscape features (i.e. the functional distance), it does not correspond directly to a physical instream distance. The modified distance is equivalent to 'functional meters'. In order to compare the distance allowed by downstream current facilitations to the distance travelled by larvae not aided by downstream currents, a second set of resistance values fixed a value of 1 for all grid cells where current speeds ranged between 0 and 10 $cm.s^{-1}$ (Table C.2). In this case, the α becomes directly equivalent to the maximal instream distance the larvae were able to travel (meters).

Table C.2 Dimensionless resistance values based on the restricting/facilitating effects of all landscape features on the connectivity in either downstream or upstream directions. Two sets of resistance values were tested to compare distances allowed with or without downstream current facilitations.

Landscape feature		Downstream resistance value		Upstream resistance value
		With current facilitation	No current facilitation	
Water depth ≤ 0m		10,000	10,000	10,000
Current speeds ($cm^3.s^{-1}$)	Speed > 0 ≤ 2	1	1	1
	Speed > 2 ≤ 4	0.3333	1	10,000
	Speed > 4 ≤ 6	0.2000	1	10,000
	Speed > 6 ≤ 8	0.1429	1	10,000
	Speed > 8 ≤ 10	0.1111	1	10,000
	Speed > 10	10,000	10,000	10,000
Drained ditches and chennalised streams		1	1	1
Exposed roads		10,000	10,000	10,000
Dense vegetation		10,000	10,000	10,000

Results revealed that during stable-high (1973) or increasing (1983) profiles between the spawning time ($Week_0$) and five weeks later during the free-swimming stage ($Week_5$), the area of effective spawning habitat reached a sill with a mobility coefficient (α) of 600 $m_{functional}$ that correspond to 1,500 m without current facilitations (Figure C.1 and C.2). When less spawning habitat areas are available at $Week_5$ during stable-low (1965) and decreasing (1998) profiles, the area of effective spawning habitat reached a sill with a mobility coefficient (α) of 150 $m_{functional}$ (=1,500 m). Interestingly, during a decreasing profile (1998), ditches and channelized streams located in drained areas allowed for a 14% (252 ha) increase in effective spawning habitats considering a larvae mobility (α) of 6000 $m_{functional}$ (= 1,500 m). Larvae located on drained ditches spawning areas have to travel a minimum of 150 $m_{functional}$ (= 600 m) to reach a nursery habitat (lines blue vs. green). The effect of roads during a stable-high profile (1973, lines green vs. red) and dense vegetation

during a decreasing profile (1998, lines red vs. orange) on the loss of effective spawning area was observed in the Figure C.1 (reduction of the effective spawning area when both landscape features were added). During a stable-low (1965) or increasing (1983) profiles, the addition of drained ditches, roads and dense vegetation did not impact the total effective spawning area.

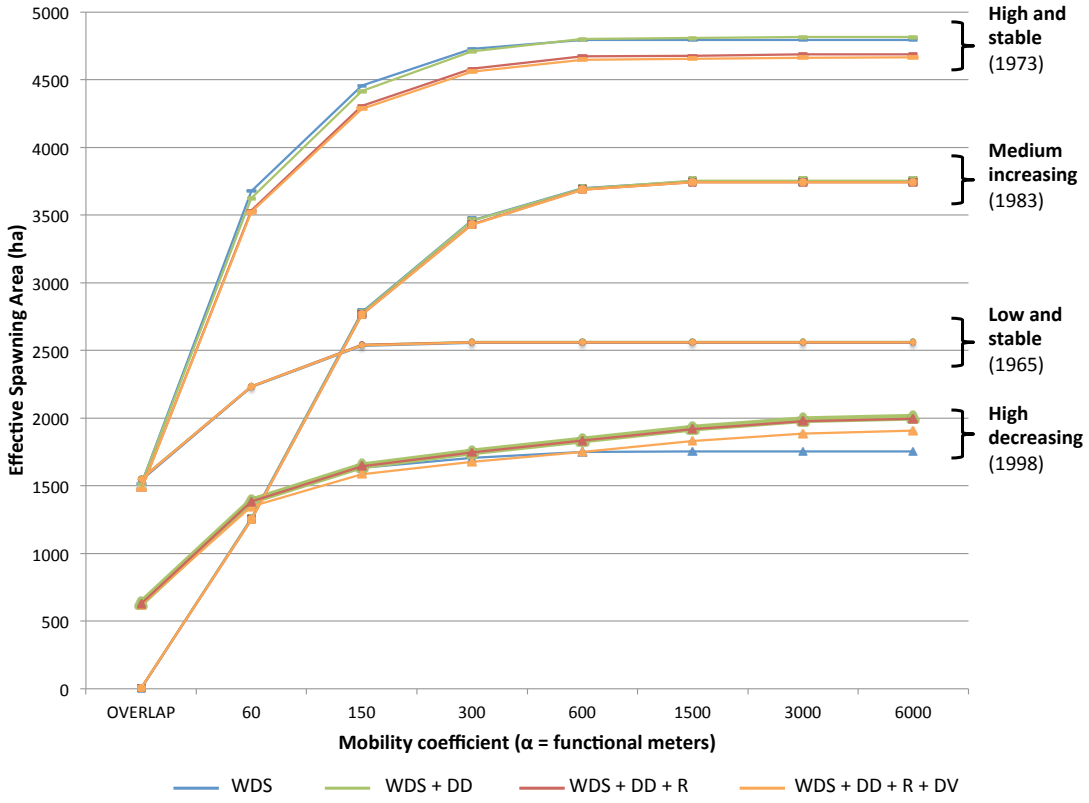

Figure C.1 Relationships between effective pike spawning surface and mobility coefficient (α) including the downstream current facilitations in the Lake St-Pierre of the St. Lawrence River for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998). The effect of the four landscape features on the total surface of effective spawning habitats was presented. They were successively added in the connectivity estimates in the following order: (1) water depth and speeds (WDS, blue color), drained ditches and channelized streams (DD, green color), roads (R, red color) and dense vegetation (DV, orange color).

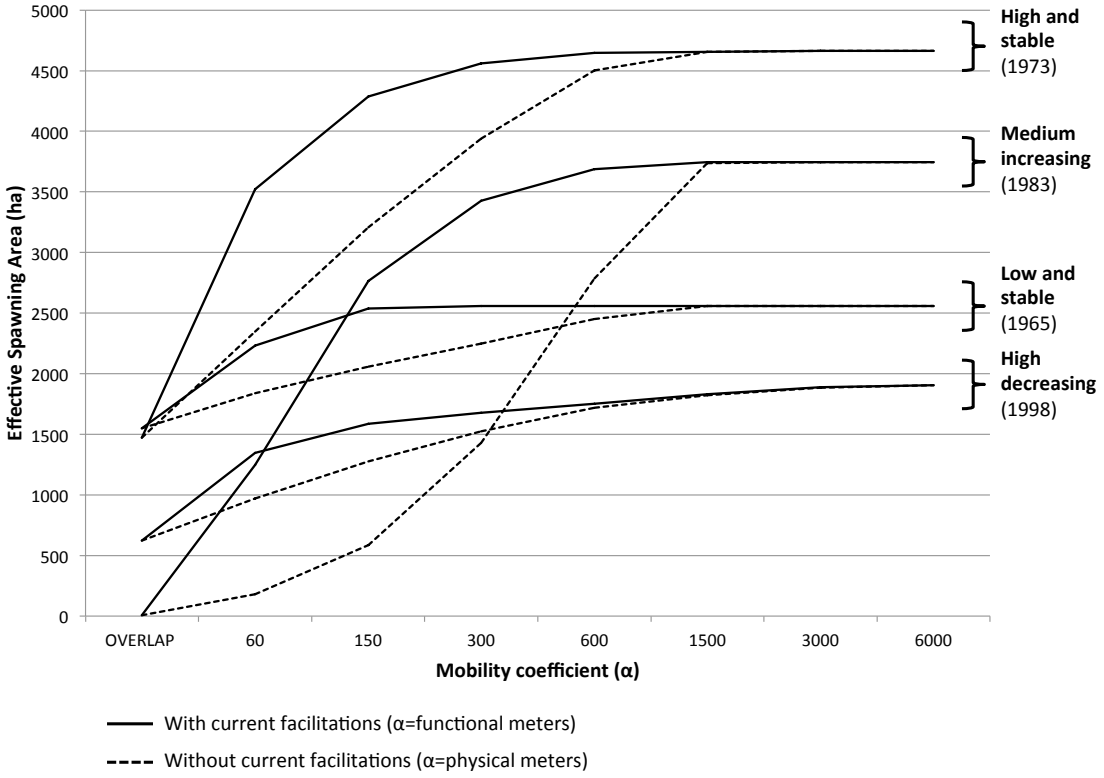

Figure C.2 Relationship between effective spawning surface of northern pike and mobility coefficient (1) with current facilitations (=functional meters, plain lines) or (2) without current facilitations (=physical meters, dotted lines) in the Lake St-Pierre (St. Lawrence, Canada) for the four hydrological profiles (stable-low in 1965, stable-high in 1973, increase in 1983, decrease in 1998). All landscape features (i.e. water depth, current speeds, drained ditches, roads and dense wetlands) are included.

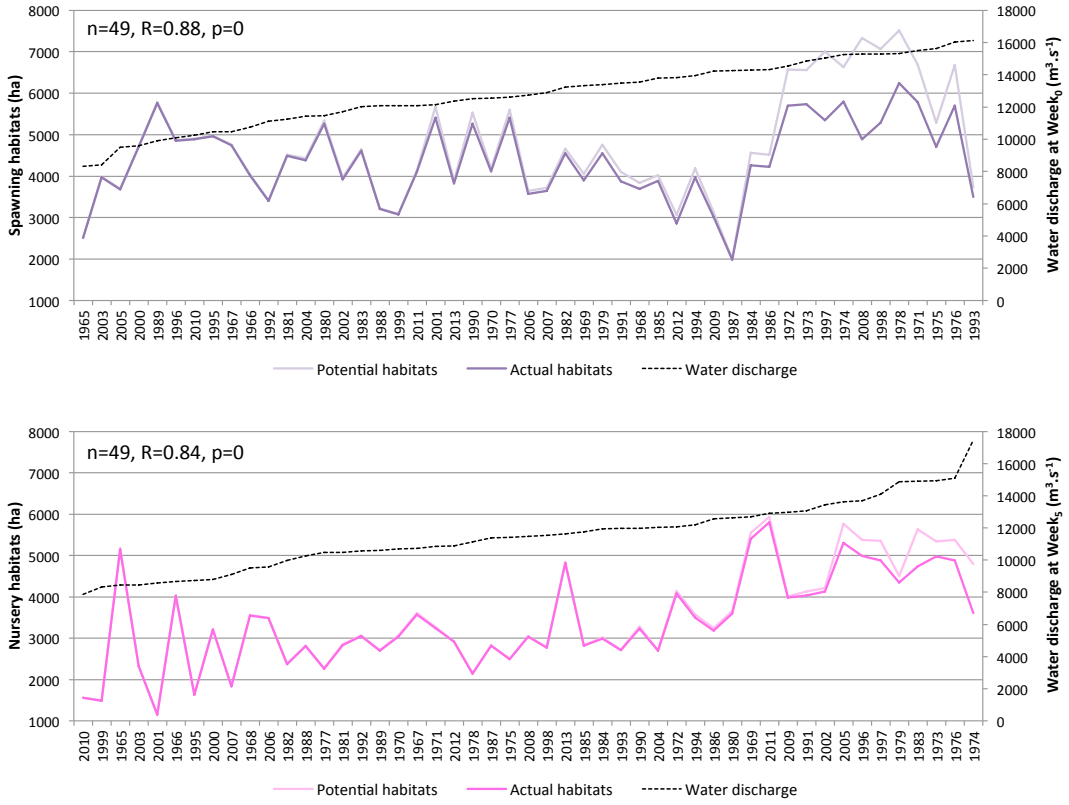

Figure C.3 Temporal values of (1) potential and (2) actual spawning and nursery habitat surfaces (i.e. including the losses generated by annual agricultural practices) according to water discharges (from lowest to highest) at the maximum spawning time ($Week_0$) and the free-swimming stage ($Week_5$) in the Lake Saint-Pierre (St. Lawrence River, Canada). The total loss of the two potential habitats modelled, either spawning or nurseries, was positively correlated with water discharges at $Week_0$ and $Week_5$ (the two *P*-value <0.05, Spearman's rank correlation). Although agricultural practices did not impact potential spawning and nursery habitats when low water discharges occurred, a water discharge >14,000 $m^3.s^{-1}$ generated the largest lost of spawning and nursery habitats areas.

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